[illegible]
231

Advances in assessment of world cephalopod resources

Progrès réalisés dans l'évaluation des ressources mondiales de céphalopodes

Progresos realizados en la evaluación mundial de cefalópodos

LIBRARY

MAY 1 0 1984

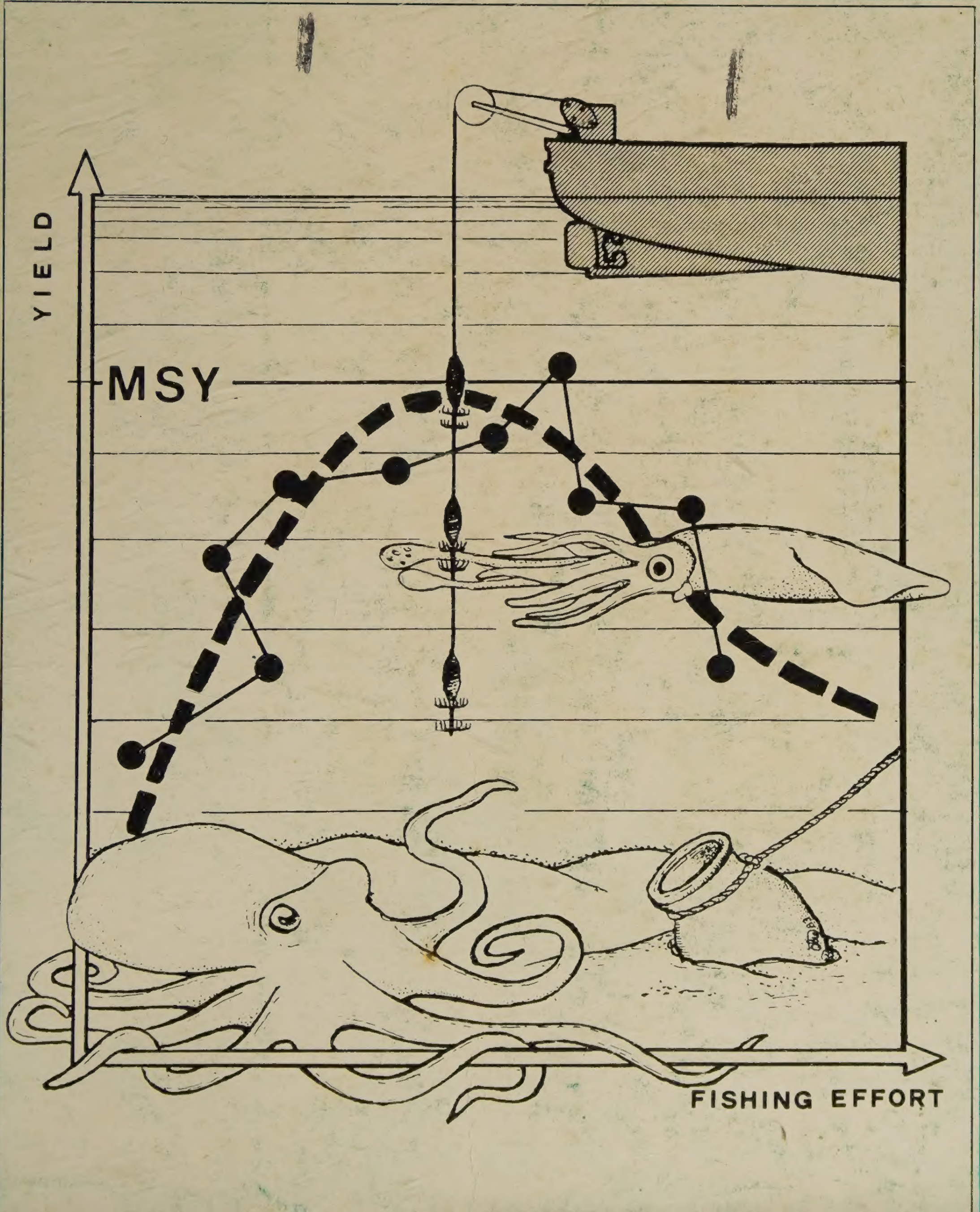
National Marine Fisheries Service
2570 Dole Street
Honolulu, Hawaii

FAO
FISHERIES
TECHNICAL
PAPER

DOCUMENT
TECHNIQUE
SUR
LES PÊCHES

DOCUMENTO
TECNICO
DE PESCA

231



FOOD
AND
AGRICULTURE
ORGANIZATION
OF THE
UNITED NATIONS

ORGANISATION
DES
NATIONS UNIES
POUR
L'ALIMENTATION
ET
L'AGRICULTURE

ORGANIZACION
DE LAS
NACIONES UNIDAS
PARA LA
AGRICULTURA
Y LA
ALIMENTACION

Advances in assessment of world cephalopod resources

Progrès réalisés dans l'évaluation des ressources mondiales de céphalopodes

Progresos realizados en la evaluación mundial de cefalópodos

Edited by
Préparé par
Publicado por

J.F. Caddy

Senior Fishery Resources Officer
Fonctionnaire principal (Ressources halieutiques)
Oficial Superior de Recursos Pesqueros

Fisheries Department
Département des pêches
Departamento de Pesca

LIBRARY
NATIONAL MARINE FISHERIES SERVICE
HONOLULU LABORATORY
P. O. BOX 3830
HONOLULU, HAWAII 96812

FAO FISHERIES TECHNICAL PAPER

DOCUMENT TECHNIQUE SUR LES PÊCHES

DOCUMENTO TECNICO DE PESCA

231

FIRM/T231

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
Rome, 1983

ORGANISATION DES NATIONS UNIES POUR L'ALIMENTATION ET L'AGRICULTURE
Rome, 1983

ORGANIZACION DE LAS NACIONES UNIDAS PARA LA AGRICULTURA Y LA ALIMENTACION
Roma, 1983

The designations employed and the presentation of material in this publication do not imply the expression of any opinion whatsoever on the part of the Food and Agriculture Organization of the United Nations concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries.

Les appellations employées dans cette publication et la présentation des données qui y figurent n'impliquent de la part de l'Organisation des Nations Unies pour l'alimentation et l'agriculture aucune prise de position quant au statut juridique des pays, territoires, villes ou zones, ou de leurs autorités, ni quant au tracé de leurs frontières ou limites.

Las denominaciones empleadas en esta publicación y la forma en que aparecen presentados los datos que contiene no implican, de parte de la Organización de las Naciones Unidas para la Agricultura y la Alimentación, juicio alguno sobre la condición jurídica de países, territorios, ciudades o zonas, o de sus autoridades, ni respecto de la delimitación de sus fronteras o límites.

M-43
ISBN 92-5-001431-7

The copyright in this book is vested in the Food and Agriculture Organization of the United Nations. The book may not be reproduced, in whole or in part, by any method or process, without written permission from the copyright holder. Applications for such permission, with a statement of the purpose and extent of the reproduction desired, should be addressed to the Director, Publications Division, Food and Agriculture Organization of the United Nations, Via delle Terme di Caracalla, 00100 Rome, Italy.

Reproduction interdite, en tout ou en partie, par quelque procédé que ce soit, sans l'autorisation écrite de l'Organisation des Nations Unies pour l'alimentation et l'agriculture, seule détentrice des droits. Adresser une demande motivée au Directeur de la Division des publications, Organisation des Nations Unies pour l'alimentation et l'agriculture, Via delle Terme di Caracalla, 00100 Rome, Italie, en indiquant les passages ou illustrations en cause.

Este libro es propiedad de la Organización de las Naciones Unidas para la Agricultura y la Alimentación, y no podrá ser reproducido, ni en su totalidad ni en parte, por cualquier método o procedimiento, sin una autorización por escrito del titular de los derechos de autor. Las peticiones para tal autorización especificando la extensión de lo que se desea reproducir y el propósito que con ello se persigue, deberán enviarse al Director de Publicaciones, Organización de las Naciones Unidas para la Agricultura y la Alimentación, Via delle Terme di Caracalla, 00100 Roma, Italia.

© **FAO** 1983

PREPARATION OF THIS DOCUMENT

Several other documents, published by FAO, are relevant to preparation of the present report: that by Voss (1973) (FAO Fisheries Circular No.149), presents early estimates of world production potential of these important marine resources. This question is also addressed by several papers in the present compilation, but the primary intention here is to expand on FAO Fisheries Technical Paper No. 173 by Okutani (1977) on the biology and assessment of those cephalopod stocks exploited by Japan in the seventies. We recognize, however, that it may be premature to attempt a definitive approach to stock assessment of cephalopods, given the limited experience to date in managing these resources and when we are still documenting the species available (see FAO Species Synopsis No. 125, Vol. 3 on cephalopods, now in preparation), and the potential market for these types of resources (Hotta: ADB/FAO/INFOFISH Market Reports, Vol. 4). The present report does, however, document some of the more promising approaches now being adopted, and should be of value to research workers entering this field.

PREPARATION DE CE DOCUMENT

Plusieurs autres documents publiés par la FAO concernent la préparation du présent rapport: celui qui a été préparé par Voss en 1973 (FAO, Circulaire sur les pêches N°149) fournit les premières estimations sur le potentiel de production mondiale de ces importantes ressources marines. Cette question est également traitée dans plusieurs documents du recueil actuel, mais le but essentiel est de développer le N° 173 FAO, Document technique sur les pêches préparé par Okutani en 1977 et qui concerne la biologie et l'évaluation des stocks de céphalopodes exploités par le Japon dans les années soixante-dix. Nous reconnaissons cependant qu'il est peut-être prématuré d'essayer de trouver une approche définitive à l'évaluation des stocks de céphalopodes, étant donné le peu d'expérience que l'on possède jusqu'ici en matière d'aménagement de ces ressources et à une époque où nous cherchons encore à inventorier les espèces disponibles (voir FAO, Synopsis sur les pêches N° 125, Vol. 3 sur les céphalopodes qui est en préparation) et le marché potentiel pour ces types de ressources (Hotta: ADB/FAO/INFOFISH Market Reports, Vol. 4). Le présent rapport cependant indique quelques-unes des approches plus prometteuses qui sont actuellement adoptées et qui devraient être utiles aux chercheurs qui se lancent dans ce nouveau domaine d'avenir.

PREPARACION DE ESTE DOCUMENTO

Hay varios otros documentos publicados por la FAO que interesan la preparación del presente informe. El realizado por Voss en 1973 (FAO, Circulares de Pesca N°149) presenta estimaciones anticipadas del potencial de la producción mundial de estos importantes recursos marinos. Esta cuestión también se trata en otros documentos de la actual compilación, pero la finalidad primordial de este documento es ampliar el N° 173 FAO, Documentos Técnicos de Pesca, por Okutani (1977), sobre la biología y evaluación de las poblaciones de cefalópodos explotadas por el Japón en los años setenta. Sin embargo, reconocemos que puede que sea prematuro intentar un enfoque definitivo de la evaluación de poblaciones de cefalópodos dada la limitada experiencia obtenida, hasta el momento presente, en la ordenación de estos

recursos y cuando todavía estamos documentando las especies disponibles (véase FAO, Sinopsis de Pesca Nº 125, Vol. 3 sobre cefalópodos), y el mercado potencial de estos tipos de recursos (Hotta: ADB/FAO/INFOFISH Market Reports, Vol. 4). No obstante, el presente informe documenta algunos de los sistemas más prometedores que se están adoptando y deberá tener cierto valor para los investigadores que trabajen en este sector.

Distribution/Distribución:

FAO Fisheries Department
FAO Regional Fisheries Officers
Selector SM

For bibliographic purposes this document should be cited as follows/La référence bibliographique de ce document doit être donnée ainsi/Para fines bibliográficos este documento debe ser citado como sigue:

Caddy, J.F. (ed.), Advances in assessment of world cephalopod resources. Progrès réalisés dans l'évaluation des ressources mondiales de céphalopodes. Progresos realizados en la evaluación mundial de cefalópods. FAO Fish.Tech.Pap./FAO,Doc.Tech.Pêches/FAO,Doc.Téc.Pesca, (231):452 p.

FOREWORD

Since the last review of world cephalopod resources by FAO (Voss, 1973), several major changes have occurred on the world fishery scene that place the cephalopods in a position of much greater visibility than formerly. These include a generally greater intensity of harvesting of shelf resources as rapid technological improvement in gear, vessels, and methods of fish detection and harvesting, which have increased the fishing power of industrial fleets; an improved versatility in utilization of new raw materials for a variety of food products, which means that unconventional resources, such as cephalopods, are finding a growing place on world markets; and last, but not least, ownership of stocks lying within 200 mi off the coast, transferred to the coastal states. Stemming from the greater intensity of harvesting there are indications that slow-growing, multi-age fish stocks are coming to share their dominance with more rapidly growing, short-lived species, among which the cephalopods occupy an important place in marine ecosystem. There is also a growing realization on the part of those scientists and fishery managers of coastal countries now responsible for management of the marine fishery resources that our knowledge of the cephalopods, their life cycles, and response to fishing is very limited. This realization is shared by managers of "developed" fishing countries in the western world where cephalopods, formerly used largely as bait, are slowly but surely coming to play an important part in local and export markets, although not yet approaching in importance their present role in several countries of Asia, in particular Japan.

PREFACE

Depuis le dernier examen des ressources mondiales de céphalopodes effectué par la FAO (Voss, 1973), plusieurs changements importants sont intervenus dans les pêches mondiales, qui rendent plus claire la situation des céphalopodes. Parmi ces changements citons: une exploitation plus intensive des ressources des plateaux car l'amélioration technique rapide des engins, des navires et des méthodes de détection et de capture ont accru la capacité des nouveaux bateaux de pêche et des embarcations existantes; une plus grande diversification dans l'utilisation des nouvelles matières premières pour toute une variété de produits de la mer signifiant que des ressources non conventionnelles telles que les céphalopodes trouvent une place sans cesse croissante sur les marchés mondiaux; et enfin, et surtout, le transfert aux Etats côtiers de la propriété des stocks à l'intérieur d'une zone de 200 mi au large des côtes. Il ressort de cet accroissement d'intensité de l'exploitation que les stocks de poissons à croissance lente et d'âges variés vont être concurrenciés par des espèces à croissance plus rapide dont la vie est brève parmi lesquelles les céphalopodes occupent une place importante. De même, les chercheurs et les directeurs des pêches des Etats côtiers, actuellement responsables de l'aménagement des ressources halieutiques renouvelables réalisent de plus en plus que nos connaissances sur les céphalopodes, leurs cycles biologiques et leurs réactions à la pêche sont très limités. C'est ce que pensent aussi les directeurs des pays halieutiques développés d'Europe occidentale où les céphalopodes, autrefois largement utilisés comme appâts, commencent lentement mais sûrement à occuper une place important sur les marchés locaux et d'exportation même si ce n'est pas encore comparable à celles qu'ils occupent dans plusieurs pays d'Asie, en particulier au Japon.

PREFACIO

Desde que la FAO realizó el último examen de los recursos mundiales de cefalópodos (Voss, 1973), se han producido cambios importantes en las pesquerías mundiales que sitúan a estos en un plano de mucho mayor interés que antes. Por regla general, entre los cambios figura una mayor intensidad de explotación de los recursos de la plataforma, mientras que el rápido mejoramiento tecnológico del equipo, las embarcaciones y los métodos para la detección y cosecha de peces ha incrementado la capacidad de pesca de las actuales y nuevas embarcaciones; hay una mayor versatilidad en cuanto a utilizar las

nuevas materias primas para una variedad de productos marinos, lo que significa que los recursos no convencionales tales como los cefalópodos, encuentran una expansión siempre más importante en los mercados mundiales; y, por último, pero non por ello menos importante, la transferencia de la propiedad de las poblaciones a los Estados ribereños dentro de 200 mi de la costa. Al ser mayor la intensidad de cosecha existe la impresión de que las poblaciones ícticas con lento crecimiento y compuestas por diversas edades están compartiendo su dominio con otras especies de corta vida con más rápido crecimiento, entre ellas los cefalópodos que ocupan un importante lugar. También hay una mayor conciencia entre los científicos y los administradores pesqueros de los Estados ribereños que actualmente se encargan de la ordenación de los recursos pesqueros renovables de que nuestros conocimientos sobre los cefalópodos, sus ciclos vitales y la respuesta a la pesca son muy limitados. Esta conciencia es compartida por los directores de los países pesqueros "desarrollados" del mundo occidental en donde los cefalópodos, que antiguamente se utilizaban en su mayor parte como cebo, están ocupando lentamente pero con seguridad un lugar importante en los mercados nacionales y de exportación, aunque no sea su función tan importante como en varios países asiáticos, especialmente el Japón.

The Editor

ABSTRACT

The present report brings together a number of separate contributions dealing with the biology, assessment and management of cephalopod resources. These illustrate individually, and as a whole, that although the cephalopods share a common environment with the dominant marine fish species, they have often adopted quite different life history strategies. These, if anything, make for a greater resistance to industrial fishing pressures than is the case for many finfish species. Several of these special features of the life history should ideally be taken into account in scientific management of both cephalopods and those fish stocks which often occur with them in the commercial catch.

RESUME

Le présent rapport groupe plusieurs articles qui traitent de la biologie, de l'évaluation et de l'aménagement des ressources de céphalopodes et montre que si les céphalopodes partagent le même milieu que des espèces plus nombreuses de poissons de mer ils ont souvent adoptées des stratégies biologiques différentes qui leur permettent de mieux résister que d'autres espèces à la pression des pêches industrielles. Plusieurs de ces caractéristiques biologiques spéciales devraient être prises en compte dans l'aménagement scientifique des céphalopodes et des autres stocks de poissons qui sont souvent pêchés en même temps qu'eux.

RESUMEN

El presente informe reúne varios trabajos recientes que tratan de la biología, evaluación y ordenación de los recursos de cefalópodos y ponen de manifiesto individual y colectivamente que, aunque los cefalópodos comparten un medio ambiente común con las especies ícticas marinas dominantes muchos peces han adoptado unas estrategias vitales completamente distintas con una mayor resistencia a las presiones pesqueras industriales de lo que sucede con muchas especies ícticas. Algunas de las características especiales del ciclo vital deberán ser tenidas en cuenta en la ordenación científica de los cefalópodos y de las poblaciones ícticas capturadas comercialmente con ellos.

CONTENTS/TABLE DES MATIERES/CONTENIDO

Page/Página

World Fisheries for Cephalopods: A Synoptic Overview (by Jean Worms) 1

Squid Resources of the Northwest Atlantic (by A.M.T. Lange and M.P. Sissenwine) 21

Stock Assessment of Cephalopod Resources in the Northwestern Pacific (by Masanao Osako and Mamoru Murata) 55

A Review of Assessment of Japanese Distant-Water Fisheries for Cephalopods (by T. Sato and H. Hatanaka) 145

Mesh Selection Study Conducted in The People's Democratic Republic of Yemen on the Cuttlefish *Sepia pharaonis* (by Michael J. Sanders and Mahmoud Bouhlel) 181

Biology of the Cuttlefish *Sepia officinalis hierredda* off the Senegalese Coast (by M. Bakhayokho) 204

Cephalopod Resources in the Indo-Pacific Region (by S. Chikuni) 264

On the Fishery and Biology of the Giant Squid *Dosidicus gigas* in the Gulf of California, Mexico (by Nelson M. Ehrhardt, Pierre S. Jacquemin, Francisco García B., Germán González D., Juan Manuel López B., Juan Ortiz C. and Agustín Solís N.) 306

Squid Maturity Scales for Population Analysis (by Marcelo Juanicó) 341

The Role of Cephalopods in the Marine Ecosystem (by T. Amaratunga) 379

The Cephalopods: Factors Relevant to Their Population Dynamics and to the Assessment and Management of Stocks (by J.F. Caddy) 416

WORLD FISHERIES FOR CEPHALOPODS: A SYNOPTIC OVERVIEW

by

Jean Worms
Marine Biological Research Centre
Université de Moncton
Moncton, N.B. E1A 3E9
Canada

ABSTRACT

In this paper the author reviews world cephalopod fisheries as a whole against total world landings of marine products by FAO statistical areas. Where possible, landings are given separately by group of species, i.e., neritic squids, oceanic squids, octopods and cuttlefish. Due to their relative importance, a more detailed account is given of the Japanese domestic and long range fisheries. The analysis of landings by species group makes clear that a shift of fishing activities is occurring from heavily exploited species (e.g., *Octopus vulgaris*, *Todarodes pacificus*) to new lightly exploited species (essentially oceanic squids) whose potential proves to be important.

RESUME

Dans cet article, l'auteur, après en avoir situé l'importance dans la pêche mondiale, dresse un tableau des prises de céphalopodes dans les différentes régions statistiques de la FAO, ventilées, quand cela est possible, par grands groupes (calmars néritiques, calmars pélagiques, octopodes et seiches). Etant donné son importance, la pêcherie japonaise fait l'objet d'un développement un peu plus long. L'analyse détaillée des débarquements par espèces met en évidence un glissement des activités de pêche des espèces traditionellement exploitées (*Octopus vulgaris*, *Todarodes pacificus*) dont les stocks sont en baisse vers de nouvelles espèces (essentiellement calmars pélagiques) peu ou pas exploitées et dont les potentiels semblent importants.

RESUMEN

En el presente trabajo, el autor, después de situar la importancia de los cefalópodos en la pesca mundial, hace una descripción de las capturas en las diferentes regiones estadísticas de la FAO, y cuando es posible, entrega los valores de capturas por grupos (calamares neríticos, calamares pelágicos, pulpos y jibias). Debido a su importancia, la pesca japonesa se analiza en forma más extensa. El análisis detallado del desembarco por especie deja ver un desplazamiento de la pesquería de las especies tradicionalmente explotadas (*Octopus vulgaris*, *Todarodes pacificus*), las cuales presentan stocks en disminución, hacia nuevas especies (esencialmente calamares pelágicos) poco o no explotadas y de las cuales el potencial de pesca parece importante.

1. INTRODUCTION

The living resources of the sea are frequently subject to heavy fishing pressure, and many coastal resources are being fished close to or even beyond the level of effort yielding the maximum sustainable yield. In the search for resources that can locally support a high level of exploitation in the near future, cephalopods must occupy a leading place, both because of their abundance and their undeniable nutritional qualities.

Besides their intrinsic interest as the most highly developed group of invertebrates which has led to numerous studies on their behaviour and physiology, we have recently seen the growth of many applied research programmes aimed at understanding the biology and response to exploitation of commercially important cephalopod species. For example, Japanese researchers have been particularly concerned with the behaviour of *Todarodes pacificus*, a species which constitutes 60-80 percent of that country's cephalopod landings. The purpose of these studies is mostly to improve the performance of fishing gear, detection techniques, etc. Studies have also been carried out on the influence of meteorological and hydrological factors on catch abundance and composition.

2. TAXONOMY AND EVOLUTION (Mangold, 1972)

Among invertebrates, cephalopods are exceptional both from their behaviour and their brain development, such that Packard (1966) notes that "....Functionally cephalopods are fish." Two important steps stand out in the evolution of cephalopods. First of all the transformation of the originally external molluscan shell into an internal skeleton, and then the use of mantle and funnel for locomotion by jet propulsions.

The table below shows the relative size of the four still existing orders of the sub-class Coleoidea.

Order	Suborder	Families or sub-families	Number of genus	Species
Sepiodea		7	20	180
Teuthoidea	Myopsida	2	9	50
	Oegopsida	28	75	200
Octopoda	Cirromorpha	3	7	25
	Incirrata	11	37	200
Vampyromorpha		1	1	1

Voss, Roper and Young (1968) give a complete classification of modern cephalopods, a classification which will be updated in the forthcoming catalogue by Roper and Sweeney (in preparation).

Among the nearly 660 species, some are nectobenthic or benthic such as most of the members of the order Sepioidea, suborder Myopsida or family Octopodida (Incirrata); others are pelagic such as members of the suborder Oegopsida, Cirromorpha and the seven families of suborder Incirrata.

Some benthonic species show an early planktonic phase which allows them as good a dispersion as for pelagic species. Strictly benthic groups however, show active speciation and great numbers of species (e.g., genus *Sepia* and *Octopus*) whereas among pelagic groups evolutive divergence seems to be the rule (many genus or even families are monotypical). This results in a number of species (pelagic or benthonic with an early planktonic stage) having a wide, almost cosmopolitan distribution with few species, and other taxes (strictly benthic) showing very local distribution patterns and high rates of speciation.

3. GEOGRAPHIC DATA

Cephalopods are found in all the oceans and seas of the world from the Arctic and the Antarctic to the tropics; from coastal waters to the high seas, and from the surface to depths of over 5 000 m. However, except in a few ocean regions, they are not subject to exploitation. Most of the large industrial cephalopod fisheries are concentrated in the northwest and central Pacific, the northwest African coasts, the Mediterranean and the northwest Atlantic.

Not all species are subject to equal fishing pressure. Most landings by weight consist of decapod cephalopods.

Although at present, cephalopods occupy all oceanic habitats from the shallows to the abyssal regions, cephalopod exploitation affects only a small fraction of this habitat and of the number of taxa available. In fact less than 10 percent of the sea surface between the shore and the continental shelf, supplies nearly 100 percent of cephalopod catches. Of these, by far the greatest proportion are benthic or neritic cephalopods, or pelagic species whose life cycle periodically brings them into coastal waters (as in the case of *Todarodes pacificus* and *Illex illecebrosus*). Therefore, a large number of species whose habitat is strictly offshore are not exploited, although several of them could constitute a commercially acceptable product.

A list of commercially exploited cephalopods would be very long, since every fishing nation has its market preferences and food traditions, and every ocean region has its own endemic geographic species or sub-species. However, even a non-exhaustive list can indicate which are the most important species on a world and local scale at the present time (Table 1).

From Table 1 it can be seen that on a global perspective, three species appear to be the most widespread and important:

Family	Species
Ommastrephidae	*Todarodes pacificus*
Sepiidae	*Sepia officinalis*
Octopodidae	*Octopus vulgaris*

With the exception of Asian countries like Japan and Korea, Canada, the Atlantic coast, the United States (California) and some countries of southern Europe (Italy, Spain) where cephalopod fisheries are practised on an industrial or semi-industrial scale, fishing for cephalopods often continues to be of a very local food character or with very local outlets and minimal processing. A description of the respective fishing methods shows that the gear used for capture of any given species varies widely and is often extremely simple.

4. THE CEPHALOPOD FISHERIES

4.1 World Evolution of the Catches

Starting in the 1960s total landings of all marine species, including cephalopods increased steadily, levelling off after 1971 at around 70 million tons (Table 2, Fig. 1), and in 1980 landings reached 72.1 million tons. Annual growth of the world catch since 1970 has averaged between one and two percent per year compared to seven percent for the 1945-70 period. Of this total, cephalopods landings account for only a small proportion; varying between 1.5 and 2.1 percent depending on the year. Since the beginning of the 1970s, cephalopod landings have fluctuated at around one million tons, most of which can be attributed to Japan.

Among cephalopods, landings of octopods (primarily *Octopus vulgaris*) made up around 170 000 t in 1980, of which over 65 percent are fished by Japan and Spain. Most of these catches come from the north Pacific (Area 61) and the West African coasts (Area 34).

Cuttlefish (mainly *Sepia officinalis* and *S. esculenta*) account for approximately 185 000 t, of which 70 000 t come from Japanese waters and 30 000 t from the northwest African coasts. Significant amounts of cuttlefish are caught in the Mediterranean (Area 37) and western Indian Ocean (Area 51).

Among squid, we should distinguish two large groups: the Loliginidae (so called "neritic squids") and the Ommastrephidae (or oceanic squids).

Stocks of the Loliginidae are probably small since they do not constitute a large part of total catches (135 000 t in 1980, i.e., 11.6 percent of total squid catches). Their importance is very local, mainly in the Mediterranean (*Loligo vulgaris*), in California (*Loligo opalescens*) and in the northwest Atlantic (*Loligo pealei*).

Table 1

List of commercially fished cephalopod species by geographic area

	Sepioidea	Teuthoidea	Octopoda
Northeast Atlantic	Sepiidae *Sepia officinalis* *S. orbignyana* *S. elegans*	Loliginidae *Loligo vulgaris* *L. forbesi* *Alloteuthis media* *A. subulata* Ommastrephidae *Todarodes sagittatus* *Illex coindetii*	Octopodidae *Octopus vulgaris* *Eledone cirrhosa*
Mediterranean	- id - Sepiolinae *Sepiola rondeletti* Rossiinae *Rossia macrosoma*	- id -	- id - *Octopus macropus*
Northwest Atlantic		Loliginidae *Loligo pallida* *L. plei* *Lolliguncula brevis* Ommastrephidae *Illex illecebrosus*	Octopodidae *Octopus maya*
Central East Atlantic	Sepiidae *Sepia officinalis* *S. bertheloti* *S. elegans* *S. orbignyana* *S. elobyana*	Loliginidae *Loligo vulgaris* *L. forbesi* Ommastrephidae *Todarodes sagittatus* *Todaropsis eblanae*	Octopodidae *Octopus vulgaris*
Central West Atlantic		Loliginidae *Loligo vulgaris* *L. plei* *Loliguncula brevis* *Sepiotheuthis sepioidea* Ommastrephidae *Illex coindetii* *Ommastrephes pteropus*	Octopodidae *Octopus vulgaris* *O. briareus* *O. macropus* *O. maya*
South East Atlantic	Sepiidae *Sepia officinalis* *Sepia* spp. *Sepiella cyanea*	Loliginidae *Loligo reynaudi*	Octopodidae *Octopus vulgaris* *Octopus* spp.

	Sepioidea	Teuthoidea	Octopoda
Southwest Atlantic	Rossiinae	Loliginidae	Octopodidae
	Rossia tenera	*Loligo brasiliensis* syn *L. patagonica* = *L. gahi* *L. ellipsura* *Lolliguncula brevis*	*Octopus vulgaris*
		Ommastrephidae	
		Illex argentinus	
Northeast Pacific		Loliginidae	Octopodidae
		Loligo opalescens	*Octopus dofleini*
		Ommastrephidae	
		Dosidicus gigas	
Northwest Pacific	Sepiidae	Loliginidae	Octopodidae
	Sepia esculenta *S. andreana* *S. latimanus* *Sepiella japonica*	*Loligo chinensis* *L. japonica* *L. beka* *L. bleekeri* *Sepioteuthis lessoniana*	*Octopus membranaceus* *O. variabilis*
		Ommastrephidae	
		Todarodes pacificus	
Central East Pacific		Ommastrephidae	Octopodidae
		Dosidicus gigas *Symplectoteuthis oualaniensis*	*Octopus vulgaris* *O. fitchi* *O. dofleini*
Central West Pacific	Sepiidae	Loliginidae	Octopodidae
	Sepia pharaonis *S. lycidas* *S. aculeata* syn *S. subaculeata* = *S. lycidas* *S. esculenta* *S. recurvirostra* *S. tigris* = *S. pharaonis* *S. latimanus* *Sepiella japonica* *Euprymna morsei*	*Loligo edulis* *L. chinensis* *L. duvauceli* *Doryteuthis singhalensis* *Sepioteuthis lessoniana*	*Octopus aegina* *Cistopus indicus*
Southeast Pacific		Loliginidae	
		Loligo gahi	
Southwest Pacific		Loliginidae	
		syn *Loligo etheridgei* = *L. chinensis*	
		Omnastrephidae	
		Nototodarus sloani	
Oceania		Loliginidae	Octopodidae
		Sepioteuthis lessoniana	*Octopus cyaneus* *O. vulgaris* *O. aegina*

	Sepioidea	Teutnoidea	Octopoda
North Indian Ocean	Sepiidae *Sepia pharaonis* *S. aculeata* *S. rostrata* *Sepiella inermis*	Loliginidae *Loligo indica* *L. hardwicki* *Sepioteuthis lessoniana* *Loliolus affinis*	Octopodidae *Octopus vulgaris* *O. globosus* *O. herdmani* *O. hongkongensis* *= dofleini*
Northwest Indian Ocean	Sepiidae *Sepia pharaonis*	Loliginidae *Loligo duvauceli* *L. edulis* *Loligo* spp. *Symplectoteuthis oualaniensis*	
Antartic		Ommastrephidae *Martialia hyadesi* *Nototodarus sloani*	Octopodidae *Pareledone* sp.

Economically the most important squids are the Ommastrephidae which account for more than one-third to one-half of total cephalopod landings (Fig. 2). Among the species exploited, *Todarodes pacificus* is subject to by far the heaviest fishing pressure. Other species like *Illex illecebrosus* off Newfoundland and *Nototodarus sloani* in New Zealand waters are also subject to intensive local fisheries.

As has been mentioned previously, only a few ocean regions contribute significantly to world cephalopod landings, and we may particularly select the following, (see Fig. 3 and Table 3) using as our main data base, national and international cephalopod landings reported in FAO (1981).

4.2 Northeast Atlantic (Area 27)

Cephalopod landings in this region are small (Fig. 4). However, in national statistics it is often difficult to separate the catches brought in from the Mediterranean and from the northeast Atlantic. This is true for both France and Spain, a large part of whose fishing activity is carried out off the Sahara coasts. However, annual cephalopod catches for the region can be estimated at approximately 29 999 t, most of which (approximately 45 percent) consisting of octopods *Octopus vulgaris* fished by Spain.

Except for the activity of Spanish boats trawling for octopods, the cephalopod fisheries in this area are still largely artisanal in character.

4.3 Mediterranean (Area 37)

For a long time the Mediterranean and Japan were the main regions where cephalopods were actively fished and sought by consumers of sea products (Fig. 5). At present, only the western basin is exploited by Spain and Italy (Worms, 1978). Production fluctuates around 52 000 t/year, most of it landed by Italian and Spanish fishermen. Each of the other countries (including France) lands less than 2 000 t/year.

Among cephalopods, octopus accounts for approximately 42 percent, cuttlefish 37 percent and squid 21 percent.

4.4 Northwest Atlantic (Area 21)

Cephalopod catches in this area have increased considerably in the past few years (Fig. 6). In fact, if we only examine squid landings in sub-area 5 and statistical area 6

Table 2

Total world landings (t) of various cephalopods (TC) and proportion of squids and cephalopods (expressed as parts/ooo) against total nominal world catch (t) of all fish, shellfish in marine and freshwater
(FAO, 1981)

	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980
C	100 600	108 500	137 300	159 100	149 548	149 886	174 742	195 969	201 140	204 668	185 471
S_1	101 300	111 100	137 400	139 700	146 226	148 950	124 349	131 350	149 664	150 237	134 077
S_2	492 100	421 400	539 700	424 700	401 138	460 688	426 667	363 951	415 383	544 167	515 916
S_3	141 200	182 100	173 800	159 600	155 561	193 255	275 409	349 809	374 567	466 895	501 382
TS	734 600	714 600	850 900	724 000	712 925	802 893	826 425	845 110	939 614	1 161 299	1 151 375
O	163 100	159 600	204 200	185 200	211 605	279 431	209 399	189 799	189 548	150 421	166 570
TC	998 700	982 700	1 192 400	1 068 300	1 074 074	1 182 510	1 210 570	1 231 498	1 330 302	1 516 387	1 503 416
NC	65 454 300	66 060 800	62 020 300	62 682 800	66 338 120	66 299 070	69 753 024	68 913 962	70 438 616	71 265 677	72 068 063
‰TS	11.2	10.8	13.7	11.6	10.7	12.1	11.8	12.3	13.3	16.3	16.0
‰TC	15.3	14.9	19.2	17.0	16.2	17.8	17.4	17.9	18.9	21.3	20.9

Key: C = cuttlefish
S_1 = neritic squids
S_2 = oceanic squids
S_3 = squids NEI
TS = total squids
O = octopods
TC = total cephalopods
NC = nominal catches
TS = proportion of squids
TC = proportion of cephalopods

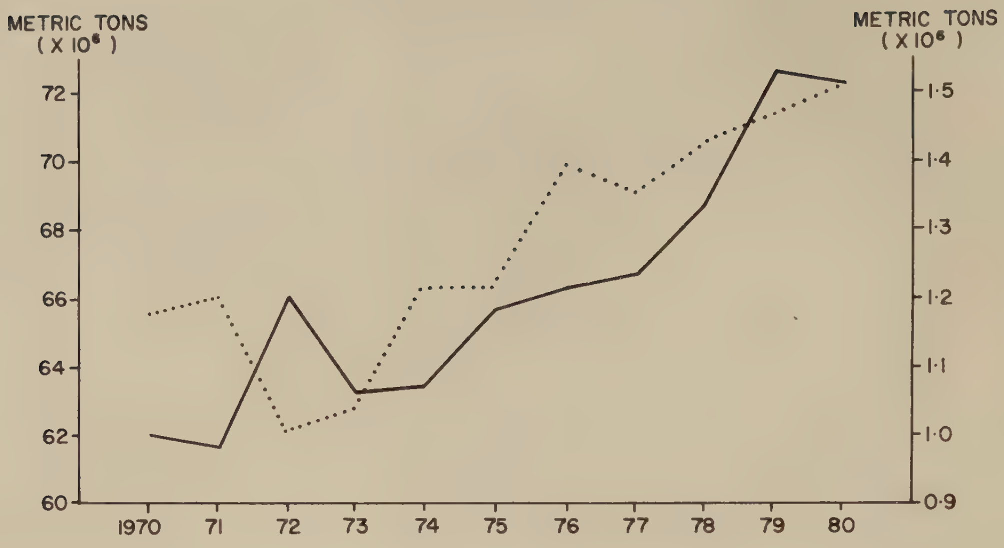


Figure 1 Historical development of world landings since 1970 in millions of tons of all marine and freshwater species including fish and cephalopods (left scale) and cephalopods separately (right scale)

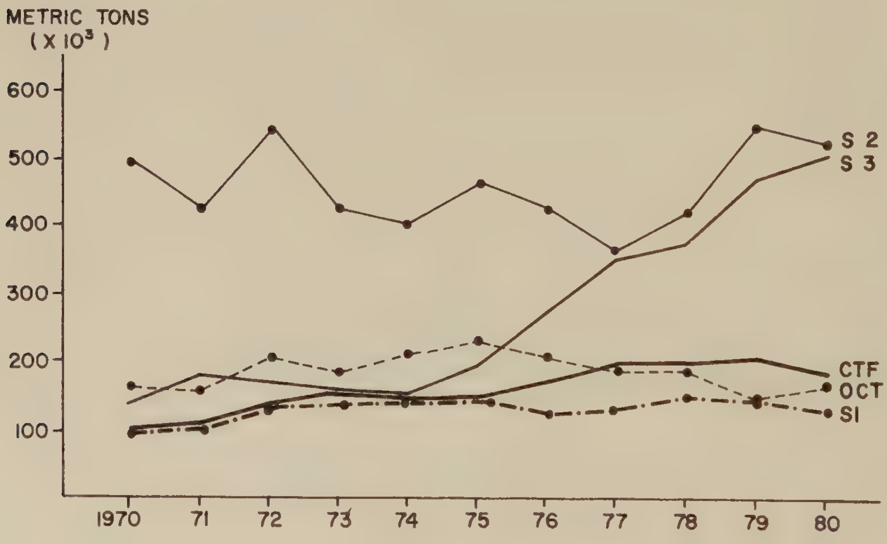


Figure 2 Historical landings in thousands of tons of cephalopods separately for neritic squids (51), pelagic squids (52), squids not elsewhere included (53), cuttlefish (C) and octopods (O) (FAO, 1981)

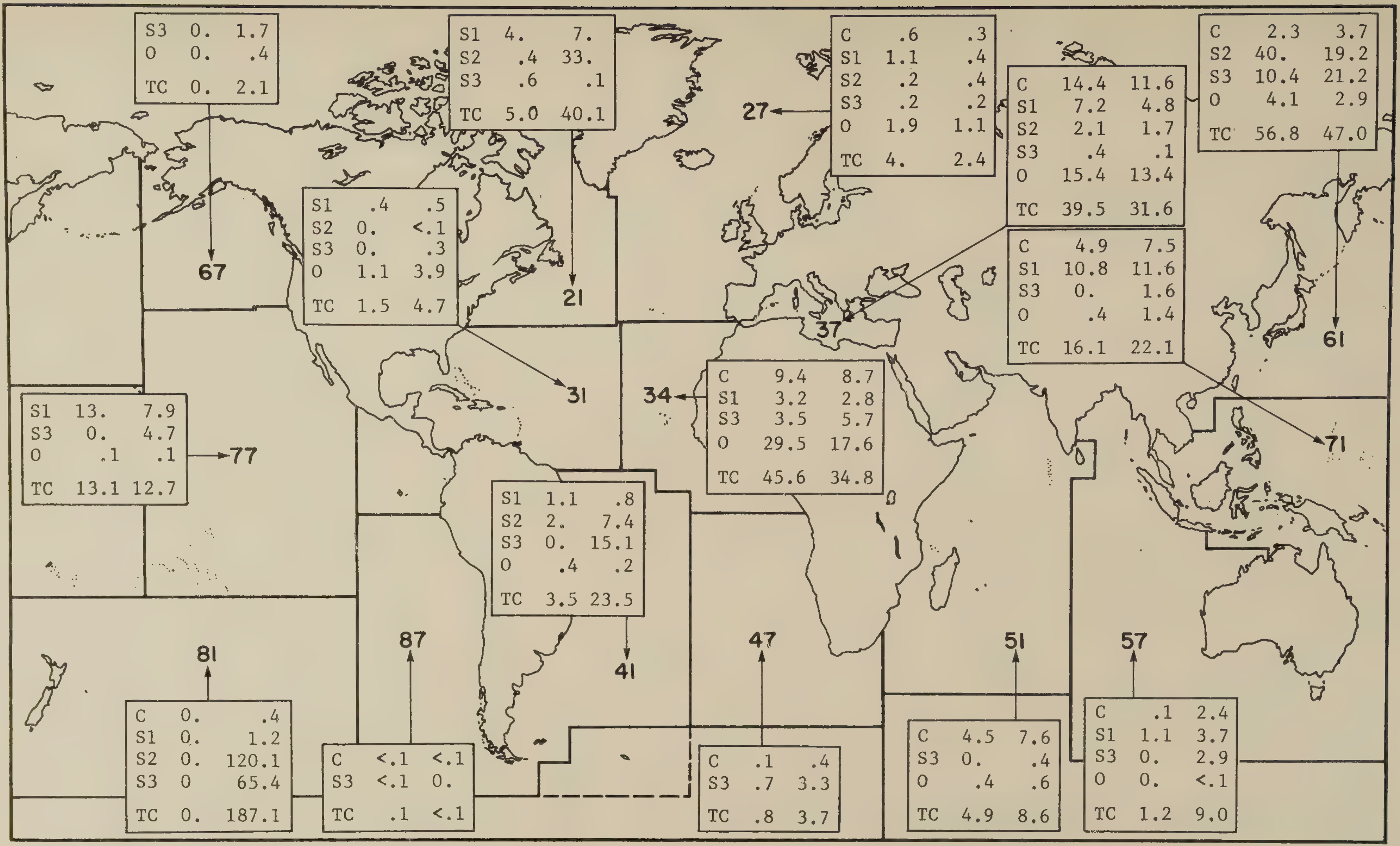

S3 0. 1.7
O 0. .4
TC 0. 2.1
67
S1 4. 7.
S2 .4 33.
S3 .6 .1
TC 5.0 40.1
21
S1 .4 .5
S2 0. <.1
S3 0. .3
O 1.1 3.9
TC 1.5 4.7
31
C .6 .3
S1 1.1 .4
S2 .2 .4
S3 .2 .2
O 1.9 1.1
TC 4. 2.4
27
C 14.4 11.6
S1 7.2 4.8
S2 2.1 1.7
S3 .4 .1
O 15.4 13.4
TC 39.5 31.6
37
C 2.3 3.7
S2 40. 19.2
S3 10.4 21.2
O 4.1 2.9
TC 56.8 47.0
61
C 4.9 7.5
S1 10.8 11.6
S3 0. 1.6
O .4 1.4
TC 16.1 22.1
71
S1 13. 7.9
S3 0. 4.7
O .1 .1
TC 13.1 12.7
77
C 9.4 8.7
S1 3.2 2.8
S3 3.5 5.7
O 29.5 17.6
TC 45.6 34.8
34
S1 1.1 .8
S2 2. 7.4
S3 0. 15.1
O .4 .2
TC 3.5 23.5
41
81
C 0. .4
S1 0. 1.2
S2 0. 120.1
S3 0 65.4
TC 0. 187.1
87
C <.1 <.1
S3 <.1 0.
TC .1 <.1
47
C .1 .4
S3 .7 3.3
TC .8 3.7
51
C 4.5 7.6
S3 0. .4
O .4 .6
TC 4.9 8.6
57
C .1 2.4
S1 1.1 3.7
S3 0. 2.9
O 0. <.1
TC 1.2 9.0

Figure 3 Distribution of world landings of cephalopods by FAO Statistical areas as a proportion (parts per thousand) of the total catch of each species (left hand column = 1970; right hand column = 1980). (FAO, 1981)

Key: S1 = Neritic squids
S2 = Oceanic squids
S3 = Squids NEI
O = Octopus
C = Cuttlefish
TC = Total Cephalopods

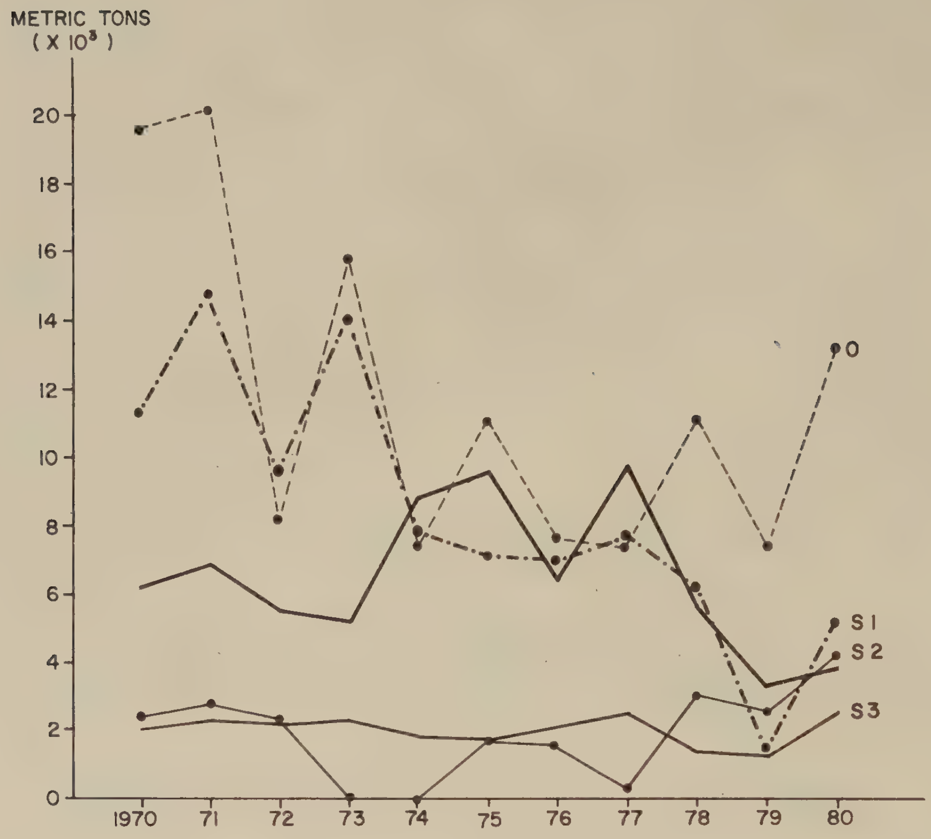


Figure 4 Annual evolution (1970-80) of cephalopods landings in FAO statistical area 27 (t x 10^3)

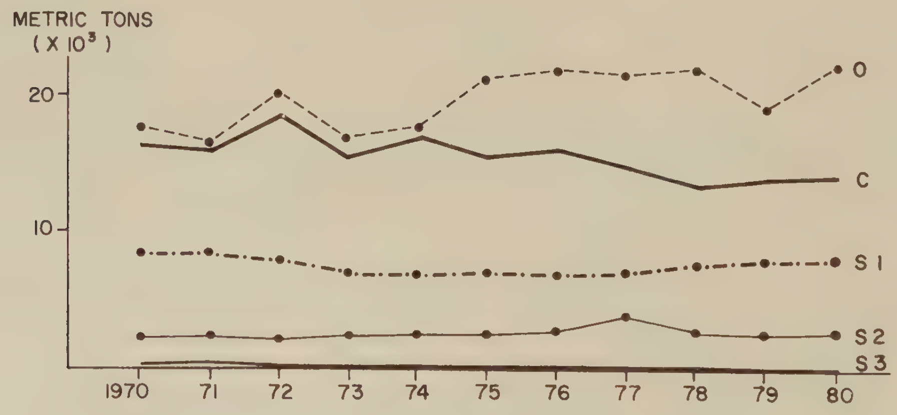


Figure 5 Annual evolution (1970-80) of cephalopods landings in FAO statistical area 37 (t x 10^3)

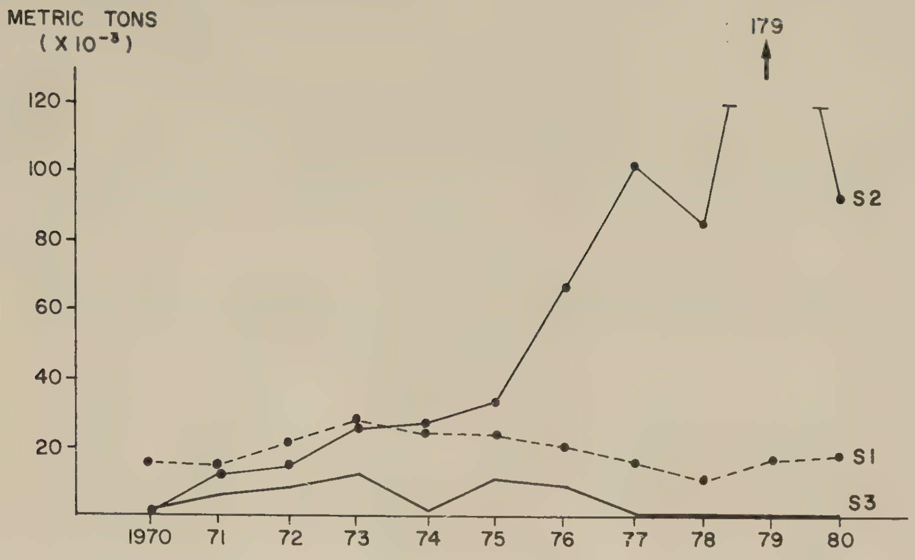


Figure 6 Annual evolution (1970-80) of cephalopods landings in FAO statistical area 21 (t x 10^3)

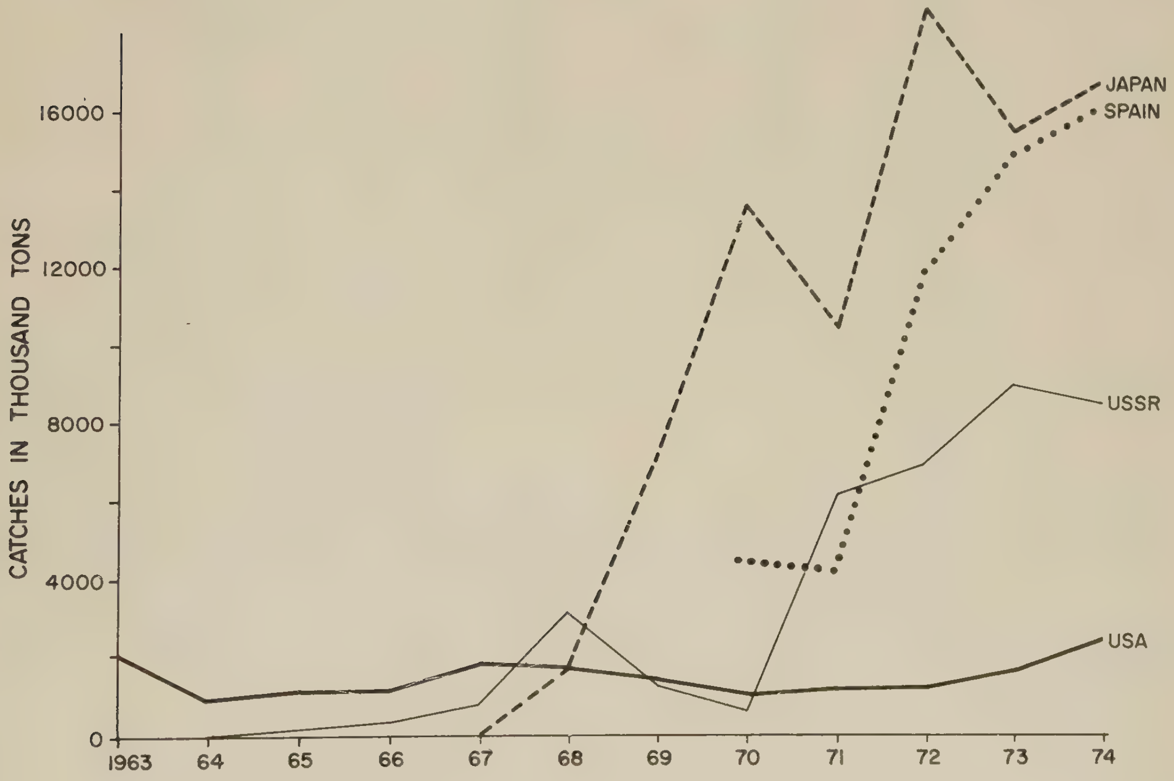


Figure 7 Annual evolution (1963-74) of cephalopod catches by the main fishing countries in the northwest Atlantic (t x 10^3) (Tibbetts, 1977)

Table 3

World landings of cephalopods by FAO statistical areas as a proportion
(parts/thousand) of the total catch for each area
(FAO, 1981)

	Area 21		Area 27		Area 31		Area 34		Area 37		Area 41		Area 51		Area 57		Area 61		Area 67	
	1970	1980	1970	1980	1970	1980	1970	1980	1970	1980	1970	1980	1970	1980	1970	1980	1970	1980	1970	1980
C	-	-	.6	.3	-	-	9.4	8.7	14.4	11.6	-	-	4.5	7.6	.1	2.4	2.3	3.7	-	-
S_1	4	7	1.1	.4	.4	.5	3.2	2.8	7.2	4.8	1.1	.8	-	-	1.1	3.7	-	-	-	-
S_2	.4	33	.2	.4	0.	<.1	-	-	2.1	1.7	2.0	7.4	-	-	-	-	40.0	19.2	-	-
S_3	.6	.1	.2	.2	0.	.3	3.5	5.7	.4	.1	0.	15.1	0.	.4	0.	2.9	10.4	21.2	0.	1.7
O	-	-	1.9	1.1	1.1	3.9	29.5	17.6	15.4	13.4	.4	.2	.4	.6	0.	<.1	4.1	2.9	0.	.4
TC	5.6	40.1	4.0	2.4	1.5	4.7	45.6	34.8	39.4	31.6	3.5	23.5	4.9	8.6	1.2	9.0	56.8	47.1	0.	2.1

	Area 71		Area 77		Area 81		Area 87	
	1970	1980	1970	1980	1970	1980	1970	1980
C	4.9	7.5	-	-	0.	.4	<.1	<.1
S_1	10.8	11.6	13.0	7.9	0.	1.2	-	-
S_2	-	-	-	-	0.	120.1	-	-
S_3	0.	1.6	0.	4.7	0.	65.4	<.1	0.
O	.4	1.4	.1	.1	-	-	-	-
TC	16.1	22.1	13.1	12.7	0.	187.1	.1	<.1

Key: C = cuttlefish
S_1 = neritic squids
S_2 = oceanic squids
S_3 = squids N.E.I.
O = octopods
TC = Total cephalopods

of ICNAF (the International Commission for the Northwest Atlantic Fisheries)[1] i.e., from Halifax in Nova Scotia to Norfolk in southern Virginia, we see a sharp rise from 2 100 t in 1963 to 55 500 t in 1974. This seems to be due mainly to the intervention of Japanese, Spanish and Russian boats, especially since 1964 (Tibbetts, 1977) (Fig. 7).

Loligo pealei tends to be a species exploited mostly for human consumption. *Illex illecebrosus* known as "bait squid" has traditionally been largely used by local fishermen for bait but is now an important food item, especially for export. Table 4 gives the tonnages captured in this region by the four main fishing countries.

Table 4

Tonnage of cephalopods captured in the Northwest Atlantic
by the main fishing countries (t)
(Tibbetts, 1977)

Year	USA	Japan	Spain	USSR	Total
1963	2 105	-	-	-	2 105
1964	929	-	-	4	933
1965	1 154	-	-	176	1 330
1966	1 173	-	-	389	1 562
1967	1 829	6	-	833	2 662
1968	1 762	1 731	-	3 176	6 679
1969	1 461	7 122	-	1 340	9 924
1970	1 061	13 639	4 510	655	19 895
1971	1 182	10 602	4 197	6 138	22 210
1972	1 207	18 691	11 860	6 976	48 707
1973	1 635	15 526	14 932	8 977	56 768
1974	2 422	16 820	16 144	8 495	55 528

Catches of different squids for the area as a whole was 110 000 t in 1980 after a tremendous year in 1979 (197 272 t).

4.5 Central East Atlantic (Area 34)

This is one of the oceanic regions where cephalopod fisheries are most active (Fig. 8). Exploitation is carried on exclusively by foreign fleets, namely Spain, Japan, USSR and Korea. In 1980, 116 000 t of cephalopods were captured off the northwest African coasts, of which 50 percent were octopods, 25 percent cuttlefish and 25 percent squid.

During the past few years we have witnessed some levelling off of catches which can be observed even more clearly for different fish species (sea bream, sparidae, etc.).

4.6 Central West Atlantic (Area 31)

In this region cephalopods (squid and octopods) are very slightly exploited (8 300 t in 1980) (Voss, 1971), which may seem surprising for Hispanic countries. Only some countries consume cephalopods, and then only very locally. However, since 1965 a considerable increase of catches have occurred, but since the collection of artisanal fisheries statistics in the scattered Caribbean Islands is very difficult, these figures should be regarded with caution (Fig. 9).

---

[1] Now replaced by NAFO (Northwest Atlantic Fisheries Organization)

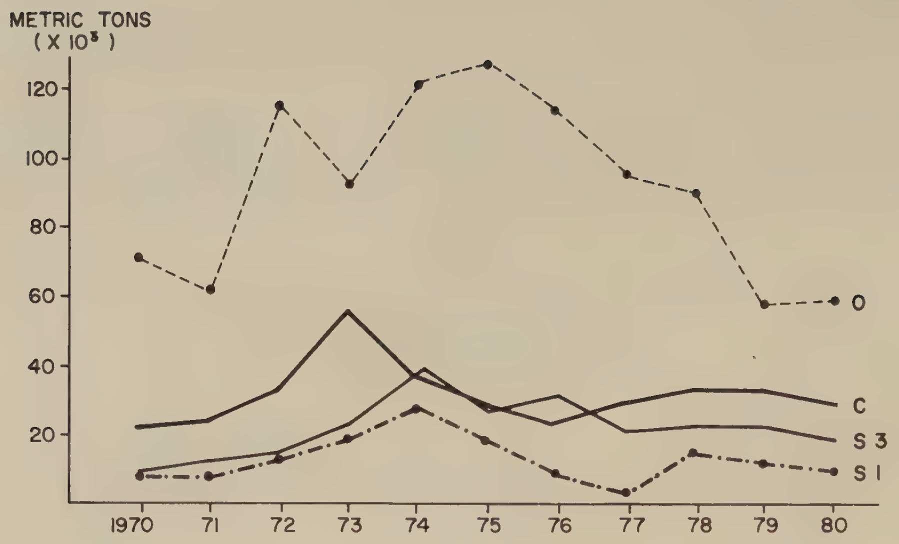


Figure 8 Annual evolution (1970-80) of cephalopods landings in FAO statistical area 34 (t x 10^3)

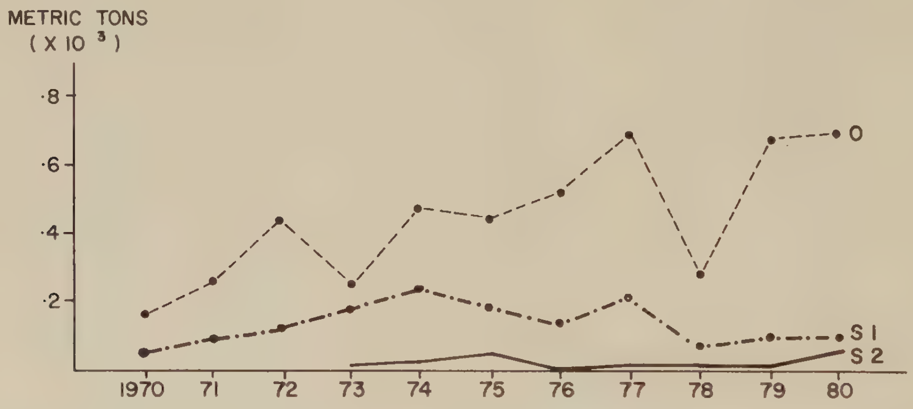


Figure 9 Annual evolution (1970-80) of cephalopod landings in FAO statistical area 31 (t x 10^3)

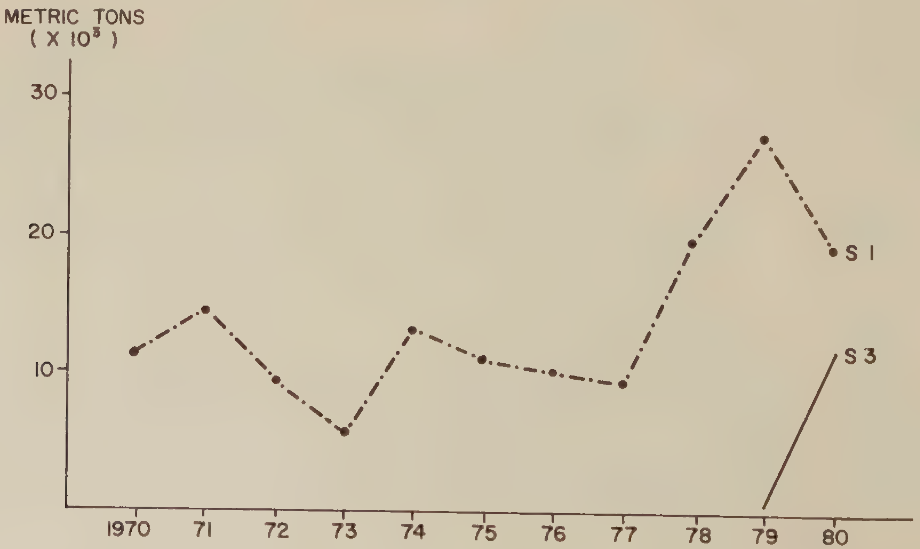


Figure 10 Annual evolution (1970-80) of cephalopod landings in FAO statistical area 77 (t x 10^3)

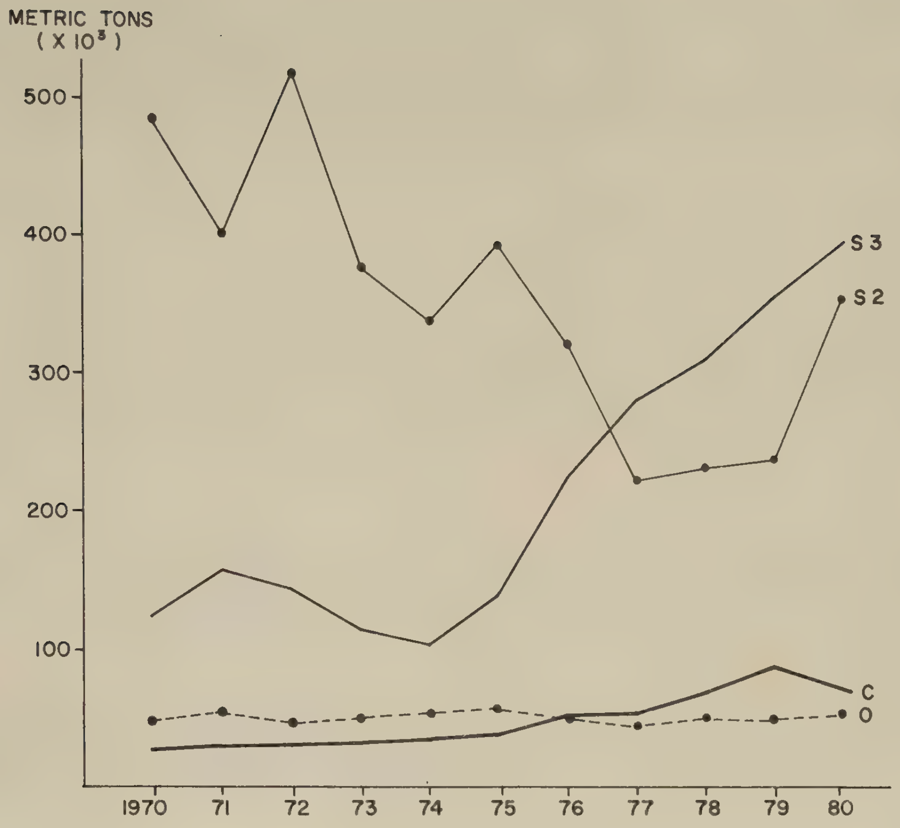


Figure 11 Annual evolution (1970-80) of cephalopods landings in FAO statistical area 61 (t x 10^3)

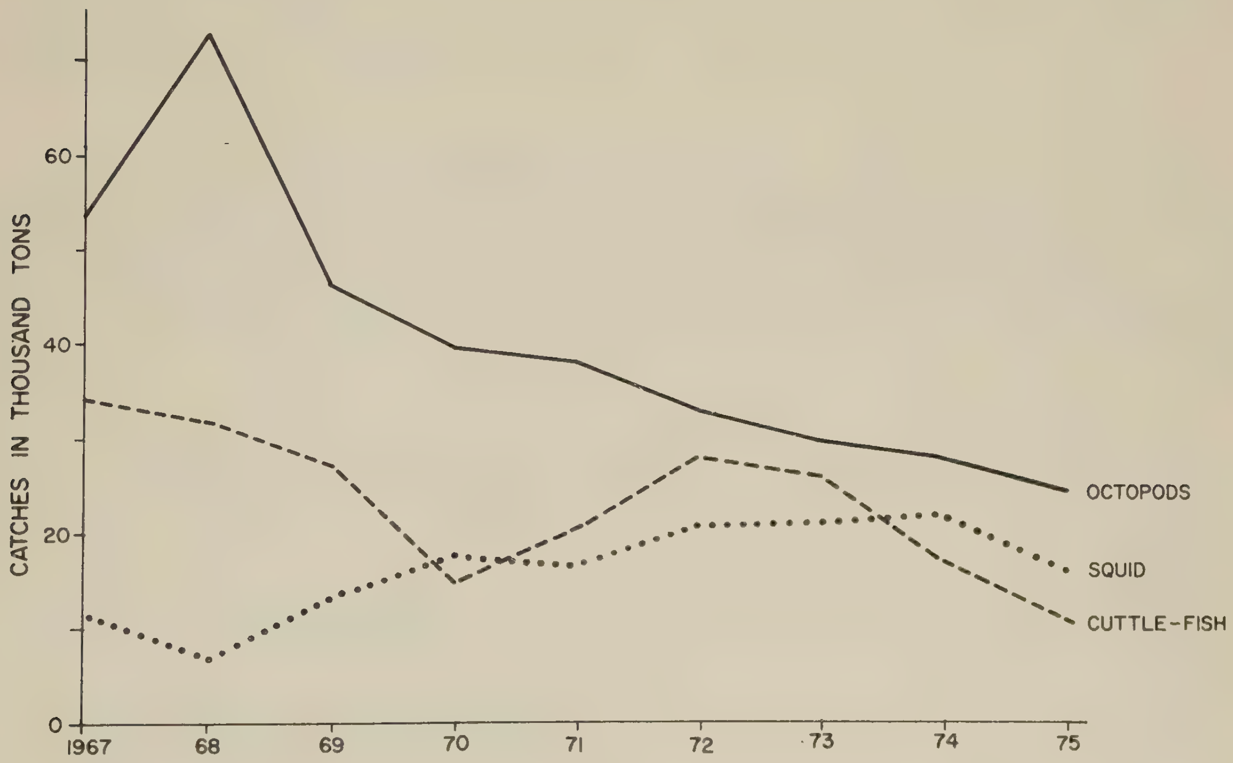


Figure 12 Annual evolution (1967-75) of Japanese distant water fisheries (thousand t) Octopods o
Squid +
Cuttlefish x

4.7 Southeast and Southwest Atlantic (Areas 41 and 47)

In these two regions cephalopod landings are still limited, although preliminary indications from research cruises suggest that potential yield is considerable. Only the ommastrephis species *Illex argentinus* is exploited on a small scale on the Argentine coast. Other species are subject to very minor fisheries. Total catches reached 40 000 t in 1980.

4.8 East Central Pacific (Area 77)

Although insignificant in world terms, the cephalopod fishery of Monterey (California), practically the only one operating in that region, is of interest at several levels. According to Fields (1965), its origin goes back at least to 1868; the date of the establishment of a Chinese fishermen's colony south of the Bay of Monterey. Furthermore, it is based exclusively on a single species *Loligo opalescens*. Total landings for this species do not exceed 20 000 t/year (Fig. 10).

4.9 Northwest Pacific (Area 61)

The Japanese fisheries are the most dynamic in the world, especially as far as cephalopods are concerned (Figure 11). Figure 12 shows the importance of their landings. In 1960, nearly 83 percent of world cephalopod catches were taken by Japanese boats. Landings from their local fishery has been dominated by a single species, *Todarodes pacificus* which accounts for 60-80 percent of Japanese catches.

The rapid development of Japanese fisheries for cepahlopods throughout the world is the result of an increase in domestic demand, such that 1968 cephalopods represented nearly one-tenth of the total landings of the Japanese maritime fishery. A threefold effort was made to promote utilization of these resources through:

(a) Study of the biology of exploited species;

(b) Improvement of fishing gear and improvement of processing methods;

(c) The systematic search for new fishing areas made it possible to exploit regions other than the northwest Pacific. Thus large cephalopod fisheries were established in the northwest Atlantic, off Africa, New Zealand and elsewhere throughout the world.

The Japanese fishery has developed significantly over the past 30 years. Until the mid-fifties, cephalopods were captured by artisanal methods from boats of less than 10 t. Subsequently, larger vessels, equipped with incandescent lighting appeared. The relationship between the shadowed area located under the boat and the optimal position of the lines was discovered and applied for greater efficiency. The other major innovation was the introduction of automatic jigging machines which, equipped with two lines, proved more efficient than one fisherman working by hand. Since their introduction, these gear have been subject to numerous specific improvements making them easier to handle.

The discovery in the 1970s of a large stock of migratory squid in the middle of the Sea of Japan (Yamato bank) lead to a sizeable increase of catches and the introduction of 100-300 gross ton boats (GTB) equipped with light-attraction mechanisms of 50 kW power, while the establishment of distant water fisheries by large vessels required the installation of freezing equipment and refrigerated holds.

Finally, on land, a major effort is being made to improve and diversify processing techniques so as to supply a demanding Japanese clientele with high quality finished products.

Although the size of the Japanese fisheries (especially in distant waters, see Fig. 12) eclipses all others, it should not be forgotten that other countries exercise considerable fishing activity in the western Pacific. South Korea lands 40 000-80 000 t of *Todarodes* per year, showing very large fluctuations from one year to another. Although it is difficult to find accurate data on Chinese landings, China probably fishes approximately 100 000 t of cephalopods per year, most of them Sepiidae spp. (mainly *Sepiella japonica*). According to the very fragmentary available data, Russian catches seem to be small (8 700 t of *Todarodes* in 1974).

With regard to the other Pacific regions we must once more mention Japanese catches in the southwest Pacific (near New Zealand) which have developed considerably since 1972).

5. FUTURE PROJECTS

It is clear from the preceding paragraphs that some of the cephalopod stocks now being exploited industrially at present are failing to provide a steady sustained yield, and declines in annual catch have occurred. The phenomenon is particularly marked for the *Todarodes pacificus* population of the waters off Japanese coasts or the *Octopus* off the northwest African coasts.

The further development of world cephalopod fisheries necessarily depends on redirecting activity to the pelagic sector. At present only the continental shelf (or less than 10 percent of ocean area) is exploited. Before contemplating an expansion, however, the economic viability of a new cephalopod fishery must be established. At present, local demand is high only in Southeast Asia and some Mediterranean regions; elsewhere it is non-existent or very low. At first it will be necessary to open new markets that can absorb large quantities of fresh or processed cephalopods. Soundly executed public advertising can lead consumers to include cephalopods in their food diet. In the United States a promotion campaign conducted jointly by the NOAA (National Oceanographic and Atmospheric Association) and the Sea Grant Marine Advisory Program seems to be producing excellent results. An extensive review of world cephalopod markets is now available (Hotta, 1982).

A survey conducted by the M.I.T. marketing centre on possibilities of introducing cephalopod-based products in the normal diet concluded by prescribing a progressive introduction of squid in the market for sea products in traditional forms of processing (croquettes, fish-sticks, etc.) and, initially, mixed with other already well accepted products (clams, shrimp, etc.).

Later, the introduction of a product exclusively composed of squid could be considered.

At present, pelagic squid Omnastrephidae are the main object of fisheries surveys carried out to determine the extent of available stocks. Under- or unexploited so far, these populations seem to offer tremendous opportunities for industrial fisheries. Estimates based on analysis of the stomach contents of certain cetaceans, and therefore considering only the species consumed by those predators, lead to figures on the order to 60-70 million t (Voss, 1973). Table 5 gives an idea of the prevailing state of under-exploitation of many stocks, and of some attractive future possibilities (Okutani, 1977)

The most promising regions include the South Pacific, the south Atlantic and the Antarctic Ocean, regions which at present, are under-exploited as far as cephalopods are concerned.

However, one should not be pessimistic concerning the heavily tapped areas like the northwest Pacific. For example, while *Todarodes pacificus* needs to be carefully monitored to avoid collapse of the stock, in the Gulf of Thailand a considerable increase of *Ommastrephes bartrami* has occurred side by side with the decrease in *Todarodes* catches.

Although some neritic species like *Sepia apama* in Australian waters and *Loligo plei* and *Loligo surinamensis* in the Caribbean, could be new targets for local small-scale fisheries, certainly the most promising possibilities are those for pelagic squid, mainly Omnastrephidae spp.

Table 5

Condition of exploitation and latent stock of the cephalopod resources in the world

Area	Catch[a] (x 10^3 t)	Local demand	Existing fishery		Major species	Possibility of increase	Possible promising species (Latent species or stock)
			Local	Long-distant			
ATLANTIC							
Northwest	50	Low	+	++	*Loligo pealei* *Illex illecebrosus*	+	*Illex illecebrosus*[b]
Northeast	250	Low	+	+	*Sepia officinalis*, *Loligo vulgaris*	++	*Todarodes sagittatus*[b]
West coast	4	Low-moderate	+	+	*Loligo pealei*	+	*Loligo plei*, *Octopus maya*
East coast	200	Very low	+	++	*Sepia officinalis*, *Loligo forbesi*	+	
Southwest	5	Low-moderate	+	-	*Loligo* spp.	+	*Illex argentinus*[b]
Southeast	2	Very low	-	+		++	*Sepia* spp.
MEDITERRANEAN	40	High	++	-	*Sepia officinalis*, *Loligo vulgaris* *Octopus vulgaris*	-	
INDIAN							
West	7	Very low	-	+	*Sepia pharaonis*	++	*Sepia pharaonis*, *Symplectoteuthis oualaniensis*[b]
East	<1	Very low	-	-		++	*Sepia* spp., *Nototodarus sloani*[b]
PACIFIC							
Northwest	240	Extremely high	+++	-	*Todarodes pacificus*[b] *Octopus vulgaris*	+	*Ommastrephes bartrami*[b]
Northeast	<1	Very low	-	-		+	*Gonatidae*[b], *Paroctopus apollyon*
West coast	120	Moderate	++	-	*Sepia* spp., *Loligo* spp.	++	*Symplectoteuthis ovalaniensis*, *Loligo* spp.
East coast	10	Low	+	-	*Loligo opalescens*	+	*Dosidicus gigas*[b]
Southwest	20	Very low	-	++	*Nototodarus sloani*[b]	++	*Nototodarus sloani*[b]
Southeast	<1	Very low	-	-		++	*Dosidicus gigas*[b]
SOUTHERN OCEAN	-	Nil	-	-		++	*Todarodes filippovae*[b] *Moroteuthis ingens*

[a] = FAO (1976), [b] = Oceanic species
(Okutani, 1977)

These species occupy an area situated between 30° and 50° latitude, north as well as south. Their biology is generally little known but good results have been obtained for *Illex illecebrosus* offshore from Newfoundland since 1973 by extrapolating the information acquired for *Todarodes pacificus* to this species.

Other not yet exploited species seem to offer promising possibilities. *Dosidicus gigas* probably constitutes enormous stocks in the east Pacific. *Symplectoteuthis oualaniensis*, already exploited in the islands of Formosa and Okinawa, has large stocks in the Indian Pacific.

To these species we may add *Berryteuthis magister* (Gonatidae spp.) in the sub-Arctic regions, *Moroteuthis ingens* (sub-Antarctic), *Illex argentinus* (southwest Atlantic), *Todarodes filippova* (sub-Antarctic), *Illex coindetti* and *Todarodes sagittatus* (Atlantic).

Briefly, although cephalopods are under-exploited world-wide, two aspects should be considered. On one hand, industrially exploited species whose stocks are endangered (*Todarodes* of the northwest Pacific, *Octopus* of the West African coasts) should be monitored, and the fishing pressure to which they are exposed should be reduced if necessary; on the other hand, there are a number of neritic or especially oceanic species that seem to offer a vast potential for future harvesting. For the latter species, better knowledge of their biology, behaviour and new approaches to harvesting and marketing these products seem essential prerequisites to their full utilization.

6. REFERENCES

FAO, 1976 Contributed papers submitted to the Expert Consultation on fishing for squid and other cephalopods. Supplement one to the report. Tokyo and Hakodate, Japan, 9-13 September 1975. FAO Fish.Rep., (170)Suppl.1:150 p. Issued also in French and Spanish

__________ 1981 Yearbook of fishery statistics. Annuaire statistique des pêches. Anuario estadistico de pesca. Catches and landings. Captures et quantités debarquées. Capturas y desembarques. 1980. Yearb.Fish.Stat./Annu.Stat.Pêches/Anu.Estad. Pesca, (50):385 p.

Fields, W.G., 1965 Structure development, food relations, reproduction and life history of the squid *Loligo opalescens* Ber. Fish Bull.Calif.Dep.Fish Game, 131:1-108 p.

Gulland, J.A., 1978 Review of the state of world fishery resources. FAO Fish.Circ., (710):41 p. Issued also in French, Spanish, Arabic and Chinese

Hotta, M., 1982 International markets for cephalopods and cephalopod products. Rome, FAO, September 1982 (mimeo)

Mangold, K., 1972 Le potentiel évolutif des céphalopodes récents. *In* Fifth European Marine Biology Symposium, edited by B. Battaglia. Padova, Piccin Editore, pp. 307-16

Okutani, T., 1977 Stock assessment of cephalopods resources fished by Japan. FAO Fish.Tech. Pap., (173):62 p.

Packard, A., 1966 Optional convergence between cephalopods and fish: an exercice in functional anatomy. Arch.Zool.Ital., 51:523-43

Roper, C.F.E. and M.J. Sweeney, FAO species catalogue. Vol.2. Cephalopods of the world. An annotated and illustrated catalogue of octopuses, squids, cuttlefishes and nautiluses of present or potential relevance to fisheries. FAO Fish. Synop., (125)Vol.2 (in preparation)

Tibbetts, A.M., 1977 Squid fisheries (*Loligo pealei* and *Illex illecebrosus*) of the North Eastern coast of the USA (1963-74). Sel.Pap.ICNAF, 2:85-109

Voss, G.L., C.F.E. Roper and R.E. Young, Classification of recent cephalopods. M.S.
1968 Institute Marine Science University of Miami

Voss, G.L., The cephalopod resources of the Caribbean Sea and adjacent region. FAO Fish.
1971 Rep., (71.2):307-23. Issued also in Spanish

____________, Cepahlopod resources of the world. FAO Fish.Circ., (149):79 p.
1973

Worms, J., Biologie et pêche des céphalopodes. 1. Techniques de pêche et de conditionnement.
1978 Pêche Marit., (1207):575-82

____________, L'exploitation des céphalopodes in Méditerranée: évolution et perspectives.
1979 Rapp.P.-V.Réun.CIESM, 25/26(10):169-84

ACKNOWLEDGEMENTS

The author would like to thank Dr. John F. Caddy, FAO Fishery Resources and Environment Division, for providing updated data on world cephalopod landings.

SQUID RESOURCES OF THE NORTHWEST ATLANTIC

by

A.M.T. Lange and M.P. Sissenwine
Resource Assessment Division
NOAA, National Marine Fisheries Service
Northeast Fisheries Center
Woods Hole Laboratory
Woods Hole, Massachusetts 02543
USA

ABSTRACT

Loligo pealei and *Illex illecebrosus* are commercially important species of the Northwest Atlantic. Small coastal fisheries expanded with the entry of distant water fleets during the late sixties and seventies. Total yield increased from a few thousand tons to over 150 000 t. Catch quotas were established in 1974 under the auspices of the International Commission for Northwest Atlantic Fisheries and have continued under extended coastal state jurisdiction.

Loligo pealei migrate to shallow waters to spawn during spring and return offshore to overwinter at the edge of the continental shelf. They are abundant from Cape Hatteras to Georges Bank. *Illex illecebrosus* are commercially abundant from New Jersey to Newfoundland. They migrate onto the continental shelf during the warmer months and migrate to deep water off the edge of the continental shelf before winter, presumably to spawn.

The spawning season of both species is protracted. Modal analysis of length frequencies indicate multiple cohorts each year. For *L. pealei*, peak spawning occurs inshore during spring, with a secondary peak during late summer and autumn. During most years, peak spawning of *I. illecebrosus* is during winter. Spawning also occurs during summer. During some years, cohorts spawned during summer dominate the fishery off the northeast USA.

Research vessel trawl surveys indicate that the abundance of both species increased significantly during the seventies. *I. illecebrosus* abundance peaked later than *L. pealei* abundance.

Yield per recruit models are modified for application to Northwest Atlantic squid. These models indicate that the yield per recruit could be increased by an increase in mesh size and by altering the seasonal distribution of fishing effort.

RESUME

Loligo pealei et *Illex illecebrosus* sont des espèces importantes du point de vue commercial de l'Atlantique nord-ouest. Les petites pêcheries côtières ont pris de l'expansion avec l'arrivée des flottilles hauturières vers la fin des années 60 et pendant les années 70. Les rendements totaux ont augmenté, passant de quelques milliers de tonnes à plus de 150 000 t. Des contingents de captures ont été fixés en 1974 sous les auspices de la Commission internationale des pêches de l'Atlantique nord-ouest et ont été maintenues en vertu de la juridiction élargie des etats côtiers.

Loligo pealei migre pour frayer dans les eaux peu profondes au cours du printemps et retourne dans les eaux côtières pour hiverner au bord du talus continental. On en trouve d'abondantes quantités du cap Hatteras à George Bank. *Illex illecebrosus* existe en grande quantité commerciale de New Jersey à Terreneuve. Il migre sur le plateau continental pendant les mois les plus chauds et dans les eaux profondes au delà du talus du plateau continental avant l'hiver, probablement pour frayer.

Pour ces deux espèces, la saison de frai est longue. L'analyse modale des fréquences de taille indique qu'il y a de multiples cohortes chaque année. Pour *L. pealei*, le frai a souvent lieu le long des côtes au printemps, le deuxième point culminant étant à la fin de l'été et pendant l'automne. La période culminante de reproduction de *I. illecebrosus* est le plus souvent pendant l'hiver. Le frai se produit également pendant l'été. Certaines années on trouve en très grand nombre les cohortes engendrées pendant l'été dans les pêcheries au large du nord-est des Etats-Unis d'Amérique.

Les prospections faites par des chalutiers indiquent que ces deux espèces ont été beaucoup plus abondantes pendant les années 70. Le nombre d'*I. illecebrosus* a augmenté plus tardivement que celui de *L. pealei*.

Les modèles de rendement par recrue sont modifiés pour être appliqués aux céphalopodes de l'Atlantique nord-ouest. Ces modèles indiquent que le rendement par recrue pourrait être augmenté par un accroissement de la dimension des mailles des filets et par une modification de la distribution saisonnière de l'effort de pêche.

RESUMEN

En el Atlántico noroeste, tienen importancia comercial las especies de calamares *Loligo pealei* e *Illex illecebrosus*. En los últimos años del decenio de 1960 y durante el de 1970 se amplió la pequeña pesca costera al entrar en operaciones las flotas de gran altura. El rendimiento total pasó de unos pocos de miles de toneladas a más de 150 000 t. En 1974, bajo los auspicios de la Comisión Internacional de Pesquerías del Atlántico Noroeste (CIPAN) se establecieron cupos de captura, que se han mantenido vigentes en virtud de la extensión de la jurisdicción de los estados ribereños.

Los calamares de la especie *Loligo pealei*, en primavera emigran hacia aguas poco profundas y vuelven mar adentro al borde de la plataforma continental para invernar. Abundan desde el cabo Hatteras hasta el Georges Bank. Desde el punto de vista comercial los calamares de la especie *Illex illecebrosus* son abundantes desde New Jersey hasta Newfoundland. Esta especie emigra hacia la plataforma continental en los meses más cálidos y regresa a las aguas profundas del límite de la plataforma continental antes del invierno, probablemente para desovar.

La temporada del desove de ambas especies es prolongada. El análisis modal de las frecuencias de talla indica la presencia de múltiples cohortes cada año. En cuanto a *L. pealei*, el desove alcanza su punto máximo en primavera cerca de la costa, y hacia finales del verano y en el otoño se produce otro período de gran desove. Casi todos los años, el desove máximo de la especie *I. illecebrosus* ocurre en invierno. También pueden producirse desoves en verano. Durante algunos años, las cohortes que proceden de desoves estivales predominan en la pesca del litoral noroeste de los Estados Unidos.

Los reconocimientos de arrastre realizados con embarcaciones de investigación indican que la abundancia de ambas especies aumentó significativamente durante el decenio de 1970. La abundancia de *I. illecebrosus* alcanzó su punto culminante más tarde que la de *L. pealei*.

Los modelos de rendimiento por recluta se modifican para su aplicación a los calamares del Atlántico noroeste. Estos modelos indican que el rendimiento por recluta se podría incrementar aumentando la luz de malla y modificando la distribución estacional del esfuerzo de pesca.

INTRODUCTION

The long-finned, winter or common American squid, *Loligo pealei*, and the short-finned or summer squid, *Illex illecebrosus*, are commercially important species of the Northwest Atlantic. Small coastal state fisheries have existed for both species off the coast of the USA and for *I. illecebrosus* off the coast of Canada since the 1800s. Catches increased sharply during the 1960s to the 1970s with the arrival of distant water fleets from Europe and Japan. Since extended coastal State jurisdiction, the catch of squid by distant water fishing fleets has declined significantly off the USA although it has increased off Canada.

This paper reviews biological aspects of exploited squid populations which are relevant to their management. Historic trends in the fishery and its management are also reviewed. In addition, the paper describes scientific methods of assessment of resource status and exploitation and management alternatives.

DISTRIBUTION

The long-finned, winter or common American squid, *Loligo pealei*, is one of two species of the genus *Loligo* and Loliginidae family, which are found off the east coast of the USA and Canada. *L. pealei* inhabits continental shelf waters from Nova Scotia to the Gulf of Mexico, with commercial concentrations occurring from southern Georges Bank to Cape Hatteras (Tibbetts, 1975). They migrate seasonally to shallow waters in the spring to spawn, staying in the warm productive shelf waters through summer and moving offshore to overwinter in deep water of less variable temperature, along the edge of the shelf.

The short-finned or summer squid, *Illex illecebrosus*, is one of three species of the Ommastrephidae family, found in the Northwest Atlantic. It is a more northern species than *L. pealei*, ranging from Greenland to Florida, with commercial concentrations from Newfoundland to about New Jersey (Tibbetts, 1975), and especially inshore in shallow waters from the Gulf of Maine to Newfoundland during the summer (Mercer, 1965).

I. illecebrosus also undergo seasonal migrations, but shoreward movements of this species are related to feeding rather than spawning. *I. illecebrosus* is found on the shelf (15-200 m depths) throughout the summer, especially in the Gulf of Maine, on Georges Bank and off Canada. In late autumn, this species moves offshore toward spawning grounds which to date are not identified, but are presumed to be in deep waters off the edge of the shelf.

The Northeast Fisheries Center conducts annual autumn (since 1963), spring (since 1968) and summer (since 1978), bottom trawl surveys on the continental shelf between 27 m and 365 m, from Cape Hatteras to the Scotian Shelf. Sampling is based on a stratified random design within a survey area which is divided into depth-latitude strata. Approximately 300 stations, allocated to strata in proportion to stratum area and randomly assigned specific locations within strata, are sampled during each survey. Catch data from these surveys are useful in describing the seasonal and annual differences in distribution of both *L. pealei* and *I. illecebrosus*.

In early spring *L. pealei* begin shoreward spawning migrations, and become available in the area south of Cape Cod by the time of the US spring bottom trawl survey (March/April, Figure 1a). Stratified mean numbers of *L. pealei* taken per survey tow from these spring surveys averaged over the period 1970-77, for the middle Atlantic, southern New England, and Georges Bank areas, by depth zone and time of day, indicate that the greatest concentrations occur in depths between 56 and 185 m (depth zones 2 and 3) for all time periods (Figure 2) in the mid-Atlantic; and generally in depths greater than 100 m (depth zones 3 and 4) in the southern New England area and on Georges Bank. *L. pealei* are not found in strata north of Georges Bank during the spring. Overall, *L. pealei* are most abundant in the mid-Atlantic, followed by southern New England and Georges Bank areas.

During late spring and summer, concentrations of mature *L. pealei* are found on the continental shelf, as illustrated by the distributions of catches from 1977 and 1978 US summer surveys (Figure 1b). Spawning occurs in shallow waters (10-25 m) from Cape Hatteras to Nantucket Shoals, and to some extent in Cape Cod Bay. The US inshore fishery is prosecuted primarily on these aggregates of spawners. Moreover, as summer progresses, smaller immature individuals probably spawned late the previous year, move inshore to feed, and are also taken in the fishery.

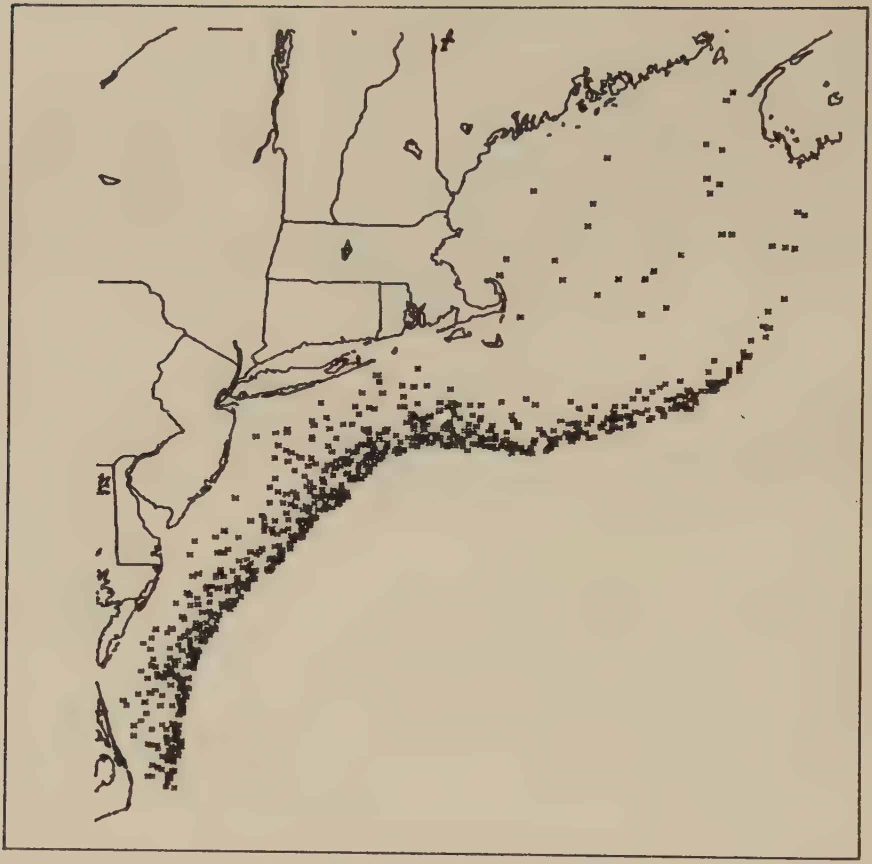


Figure 1a Distribution of *L. pealei* from US bottom trawl surveys in spring (1968-78)

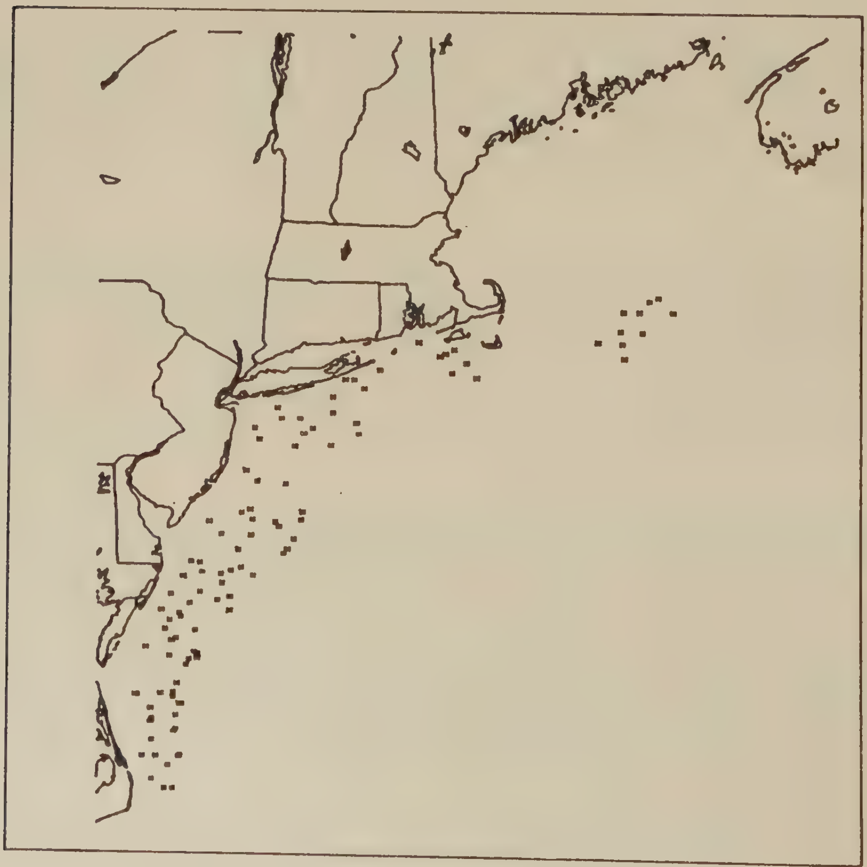


Figure 1b Distribution of *L. pealei* from US bottom trawl surveys in summer (1969, 1977 and 1978)

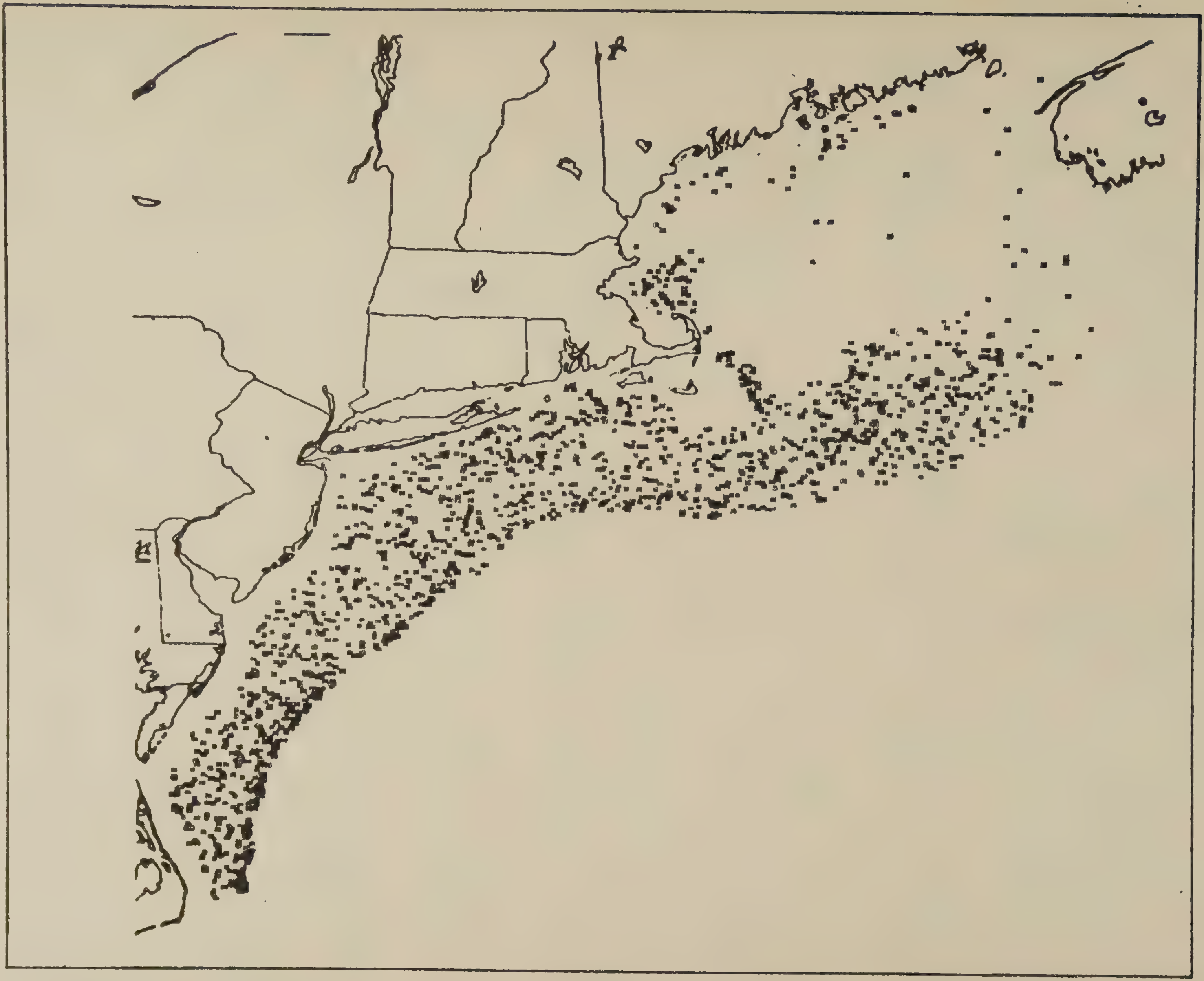


Figure 1c Distribution of *L. pealei* from US bottom trawl surveys in autumn (1967-78)

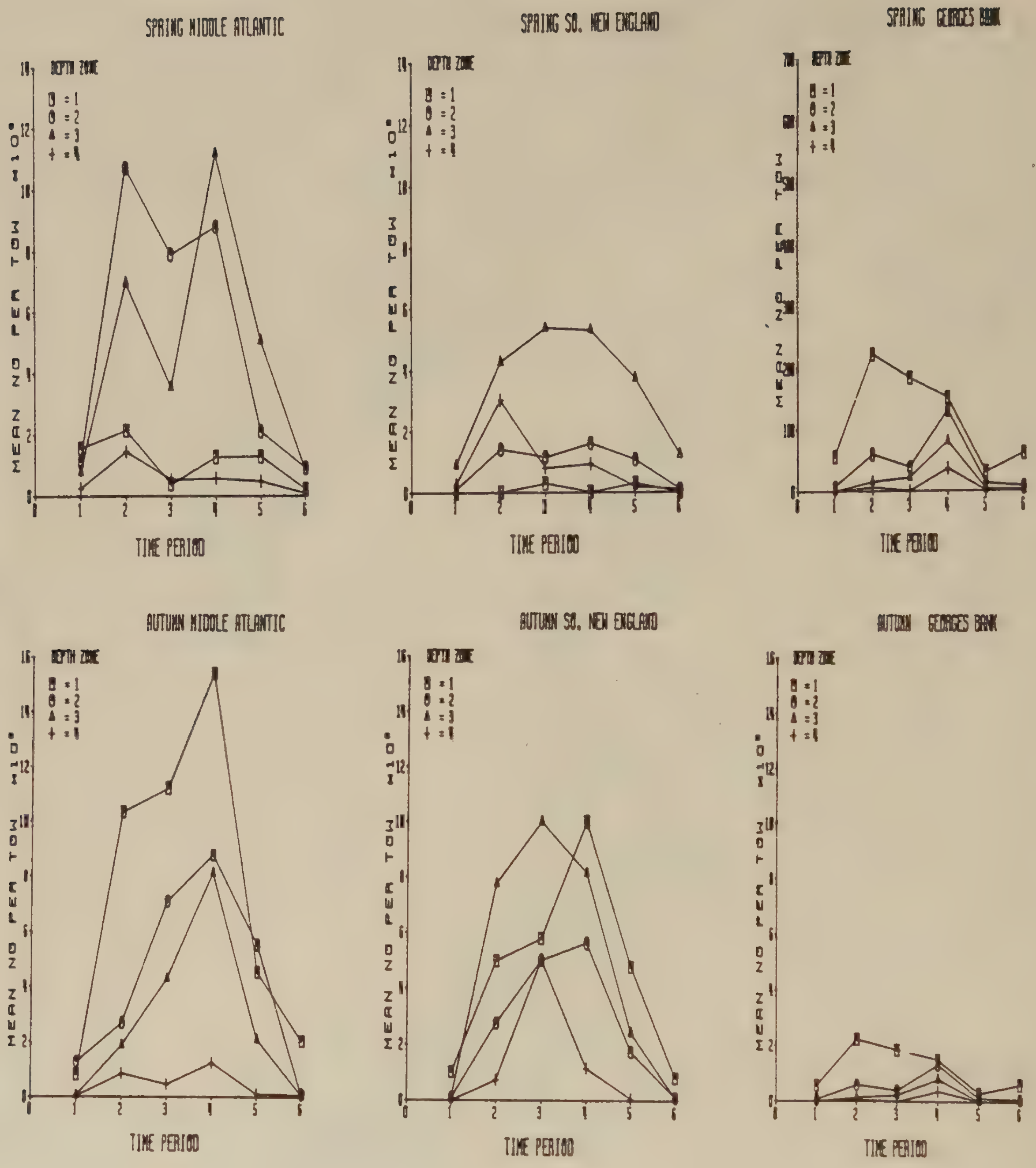


Figure 2 Mean catch (number) per tow of *L. pealei* from US bottom trawl surveys (1970-77), by season, area, depth and time of day.
Depths: 1 - 27 to 55 m; 2 - 56 to 110 m; 3 - 111 to 185 m; 4 - over 185 m.
Times: 1 - 00.01 to 04.00 h; 2 - 04.01 to 08.00 h; 3 - 08.01 to 12.00 h; 4 - 12.01 to 16.00 h; 5 - 16.01 to 20.00 h; 6 - 20.01 to 24.00 h

In the late summer and early autumn, offshore migration begins, and by the time of the US autumn bottom trawl survey (September/November), *L. pealei* are found over the shelf in all depth zones from Georges Bank, south (Figure 1c). The greatest mean catches per tow of *L. pealei* during the autumn survey (Figure 2) were again taken in the middle Atlantic area, primarily inshore in depths from 26 to 55 m (depth zone 1). In southern New England strata, the largest catches were taken further offshore in 111 to 185 m (depth zone 3), though significant catches were still taken in shallower waters. At this time, on Georges Bank and in the Gulf of Maine, *L. pealei* are still found in more shallow (26-110 m zones 1 and 2) waters, though overall catches are much less than in the areas to the south.

Differences in *L. pealei* availability are also exhibited among times of day (Figure 2) with catches (in numbers) from bottom tows, between 04.01 to 16.00 h (time periods 2, 3 and 4), generally greater than from 16.01 to 04.00 h (time periods 5, 6 and 1) in all three areas. These differences indicate diel differences in vertical distribution which may be related to feeding as great numbers of smaller individuals move toward the surface and out of the path of the trawl to feed at night. Roper and Young (1975) describe this diel dispersion for several Loliginidae species.

Sissenwine and Bowman (1978) have also shown this difference when, in analysis of catches from autumn gear mensuration cruises, they found daytime (06.00-16.00 h) catches in weight were greater than night catches by a factor of 2.87. Their analysis also indicated the daytime catch in numbers to be 18.9 times the night value. This 18.9 to 2.87 difference in numbers to weight implies differential vertical migration by size, i.e., smaller individuals more readily move off bottom at night. Summers (1967) found that water temperature influences the distribution and abundance of *L. pealei*, with major catches restricted to areas with bottom temperatures of 8°C or higher in the winter.

Lange (MS 1980) found that the greatest US survey catches of *L. pealei* were taken at bottom temperature ranges of 10°-13°C in the spring and 10°-17°C in the autumn. Catches in the strata where bottom temperatures were greater than 17°C were never as low as the minimums found in the cooler temperatures.

I. illecebrosus occurs over a broader range of water temperatures than *L. pealei*, from 0° to 15°C, with peak occurrence at 7°-13°C (Roper and Lu, 1979). Location of over wintering (and spawning) grounds and details of the life history of this species are not yet known. It is believed that spawning occurs off the edge of the continental shelf in winter and spring off Canada, while recent observations of *I. illecebrosus* larvae and juveniles off Cape Hatteras and northward to Georges Bank, during all seasons, indicate that spawning takes place over and extended period, possibly year around (Roper and Lu, 1979) off the USA. *I. illecebrosus* is taken only occasionally during the spring bottom trawl survey (March/May), in deep water (Figure 3a), as most of the stock is apparently further offshore. Comparison of mean catches per tow, in numbers, for each area and depth zone, by time of day indicate that in spring, *I. illecebrosus* are at depths greater than 110 m (depth zones 3 and 4) and are more susceptible to trawl gear between 04.01 and 16.00 h, though diel differences in availability to trawl gear are not as significant as for *L. pealei* (Sissenwine and Bowman, 1978).

In summer, *I. illecebrosus* move onto the shelf (Figure 3b) where the commercial fishery occurs. Along the northern New England coast and off Nova Scotia and Newfoundland in Canadian waters, *I. illecebrosus* continues movement onto the shelf to shallow waters, probably in search of food, through July, August and September.

I. illecebrosus are found throughout the range of the US bottom trawl survey during the autumn (Figure 3c), from Nova Scotia to Cape Hatteras, and from shallow waters to the shelf edge. However, though mean catches per tow are much greater than during the spring, the catch rate of *I. illecebrosus* in this area is generally well below that of *L. pealei*. This is related to the lower catchability of this species by bottom trawls compared with *L. pealei* (Sissenwine and Bowman, 1978). However, since 1978, catch of *I. illecebrosus* by weight has increased to levels comparable to those of *L. pealei* (Figure 4). During the autumn the greatest catches of this species are made in the middle Atlantic and southern New England areas, at depths greater than 185 m (depth zone 4). Overall, catches in the areas to the north, on Georges Bank and in the Gulf of Maine, are lower than to the south, but *I. illecebrosus* if found in these northern areas, in significant quantities into shallow depths of 56 m (Figure 4). Diel differences in catches per tow from depth zone 4 (over 185 m) during autumn were evident in all areas, with greatest values found between 04.01 and 16.00 h. Roper and Young (1975) also found *I. illecebrosus* concentrating on the bottom in daytime and dispersing through the water column at night.

Dawe, Beck and Drew (1981) reported greatest catches from a mid-water trawl survey (February/March, 1981) in the slope water and Gulf Stream south of the Grand Banks, to be during night and dawn (19.01-09.00 h), supporting the observation of movement of *I. illecebrosus* into the water column at night. Lange (MS, 1980) found that in spring the

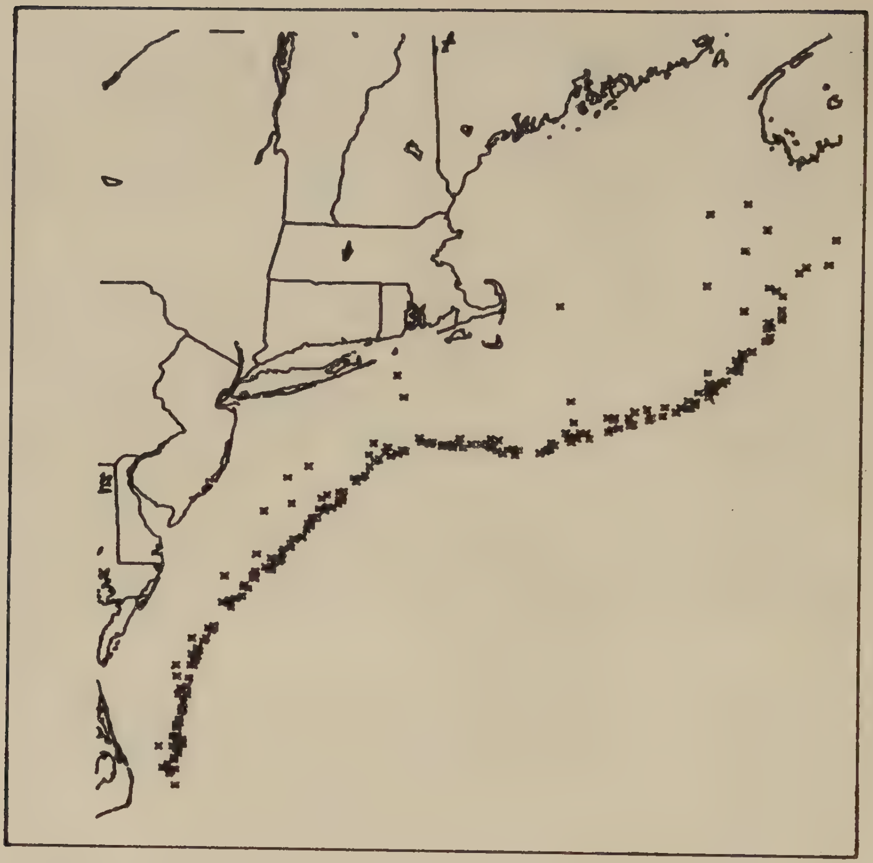


Figure 3a Distribution of *I. illecebrosus* from US bottom trawl surveys in spring (1968-78)

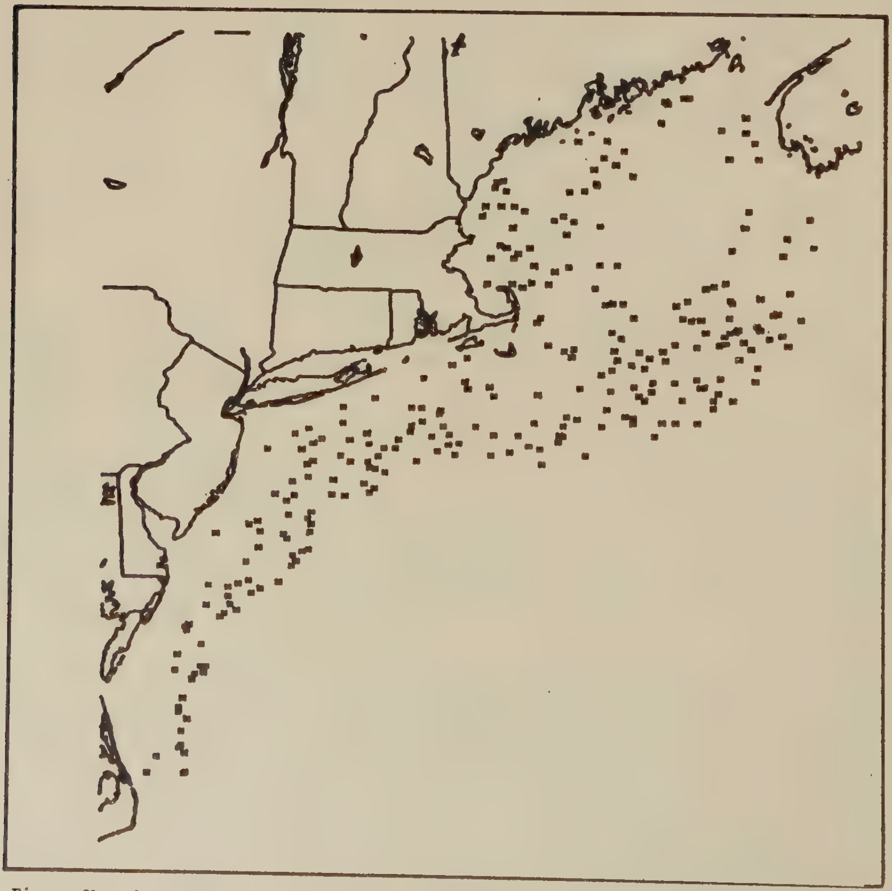


Figure 3b Distribution of *I. illecebrosus* from US bottom trawl surveys in summer (1969, 1977 and 1978)

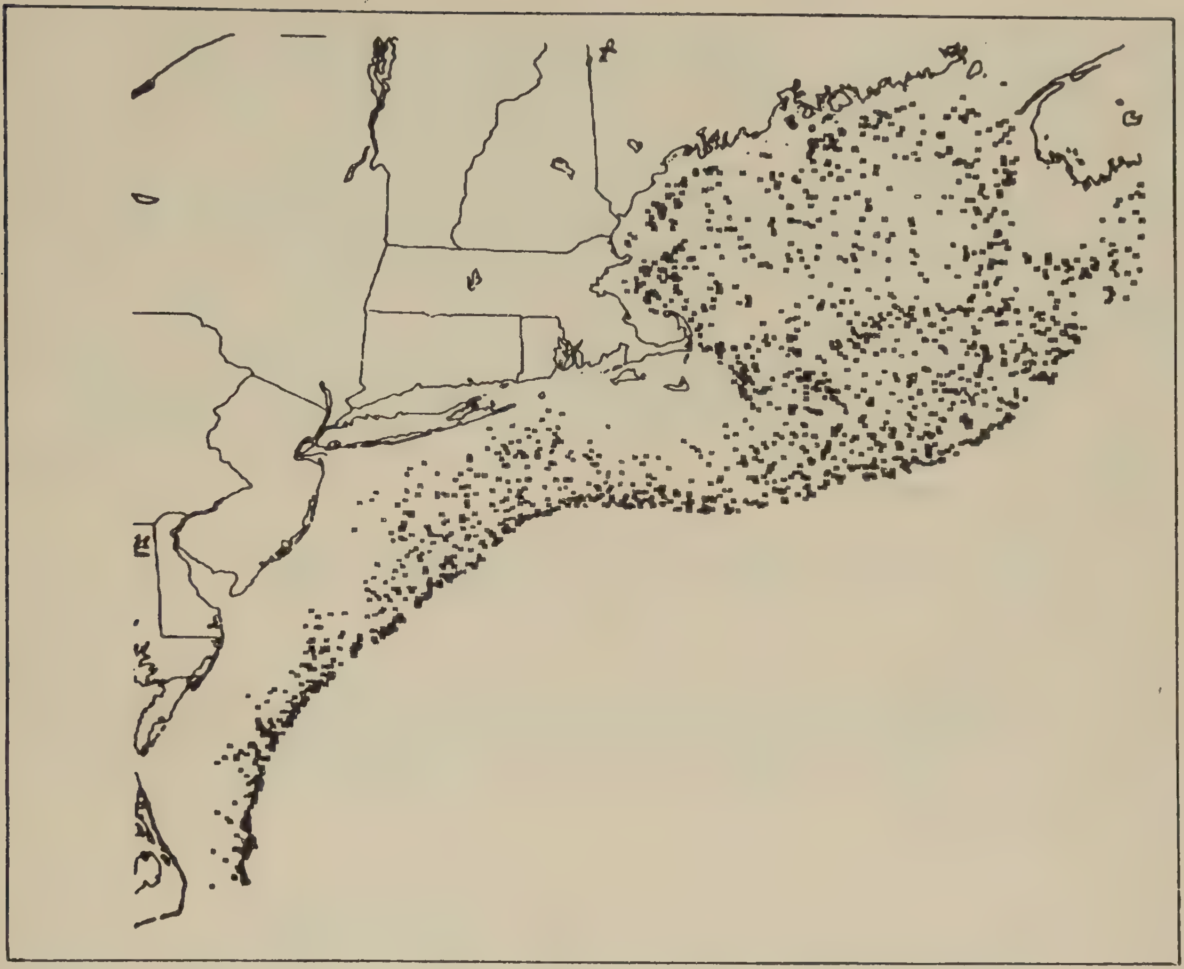


Figure 3c Distribution of *I. illecebrosus* from US bottom trawl surveys in autumn (1967-78)

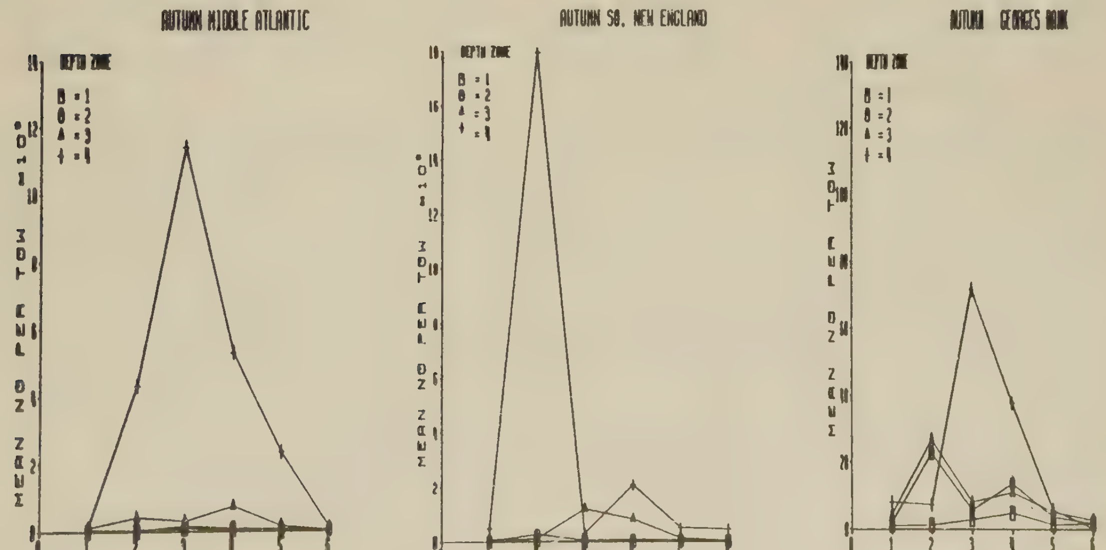


Figure 4 Mean catch (number) per tow of *I. illecebrosus* from US autumn bottom trawl surveys (1970-77), by area, depth zone and time of day (time and depth codes as for *L. pealei*)

greatest abundance of *I. illecebrosus* is in areas where temperatures are greater than 10°C (10°-16°C) while in autumn, *I. illecebrosus* were most abundant in temperatures between 7° and 13°C. Analysis of size distribution by depth and area, off the USA (Lange, MS 1980), indicate that in spring the mean size of captured *I. illecebrosus* is greater with increased depth, and that the largest individuals were found in the southern New England area. Again, in autumn, the larger individuals were found in the greatest depth zone, but they were also found further north, to Nova Scotia, while the smallest specimens were taken in the middle Atlantic and southern New England areas. Canadian surveys (Koeller, 1980) on the Scotian Shelf indicate that in summer (July) *I. illecebrosus* is distributed over most of the shelf, with concentrations in the Central LaHave and Emerald Basin areas and along the edge of the continental shelf. *I. illecebrosus* were found at depths ranging from 33 to 350 m with all large (>100 kg) catches taken between 110 and 183 m. The distribution of *I. illecebrosus* from Canadian surveys in September, in the Gulf of St. Lawrence is well defined, along the edge of the Laurentian Channel between 91 and 183 m (Koeller, 1980). The occurrence of squid in the shallower water of the southwestern Gulf is rare. Mean lengths in the Gulf were always larger than on the shelf though this is probably due to additional growth between July and September.

THE SQUID FISHERY

Historical Fishery

The squid fishery has been prosecuted in US waters, from Maine to North Carolina, since the late 1800s (Lyle, 1968; Table 1). Initially, both *L. pealei* and *I. illecebrosus* were taken only incidentally by US summer otter trawl fisheries, and to some extent in the inshore Massachusetts trap fisheries. Most catches, if not discarded, were used as bait for fishing for cod, and even today much of the US catch goes to the market as bait. However, small food markets did develop for fresh or frozen squid in cities as Boston, New York and Philadelphia.

This fishery produced average annual landings of 1 232 t in the New England area and 700 t in the middle Atlantic area, from 1928 through 1963 (the last year that the USA was the only country reporting squid catches). These catches were never reported by species, though it is assumed that most catches in the middle Atlantic were long-finned squid (*L. pealei*) and that catches north of Cape Cod were short-finned squid (*I. illecebrosus*).

An *I. illecebrosus* fishery of similar magnitude (used primarily for bait), developed off Newfoundland and Nova Scotia, Canada (Mercer, 1973; Table 2), in the early 1900s. This fishery is prosecuted inshore during the summer months. Squid jigging was the method most frequently employed by local Canadian fishermen, and still accounts for a significant portion of the inshore landings in that area.

The first year of reported distant water fleet squid catches in the Northwest Atlantic was 1964 (Table 3). Squid catches incidental to other Soviet fisheries, were the only reported distant water fleet squid catches until the winter of 1967, when Japan began an exploratory trawl fishery for long-finned squid (Ikeda, Nagasaki and Imanaga, 1975), in ICNAF subarea 5 and statistical area 6 (Figure 5). Japan has taken a major portion of the *L. pealei* catch since the beginning of its directed fishery. Spain entered the squid fishery in the 1969-70 season, remaining in the Northwest Atlantic through the summer of 1970, to begin a directed fishery for short-finned squid in the same waters where it had taken long-finned squid the previous winter. Italy first participated in this directed fishery in 1972, reporting catches of 2 000 t of *L. pealei* and 1 200 t of *I. illecebrosus* that year.

Although Japan had always taken quantities of short-finned squid in conjunction with its long-finned fishery, it was not until 1973 that it began a summer-autumn exploratory trawl fishery for *I. illecebrosus* (Ichikawa and Sato, 1975), in the waters from Cape Hatteras to Newfoundland. Since that time they have conducted directed fisheries on both species.

Table 1

US landings[a/] of squid, in t, 1879-1967, from the New England and middle Atlantic regions[b/]

Year	New England	Middle Atlantic	Total
1887	231.8	-	231.8
1888	220.5	-	220.5
1889	257.6	17.7	275.3
1890	-	17.7	17.7
1891	-	18.6	18.6
1897	-	68.5	68.5
1898	546.6	-	546.6
1901	-	90.3	90.3
1902	2493.4	-	2493.4
1904	-	72.6	72.6
1905	428.6	-	428.6
1908	977.9	131.6	1109.0
1919	2956.1	-	2956.1
1921	-	346.5	346.5
1924	1395.7	-	1395.7
1926	-	714.9	714.9
1928	3595.6	-	3595.6
1929	2561.0	409.1	2970.1
1930	2497.5	804.7	3302.2
1931	1275.1	994.7	2269.8
1932	1365.3	998.4	2363.7
1933	487.6	359.2	846.9
1934	-	-	-
1935	1607.5	1098.6	2706.1
1936	-	-	-
1937	1494.6	1067.3	2561.9
1938	976.6	928.5	1905.1
1939	1088.6	1496.9	2585.5
1940	794.7	1188.4	1983.1
1941	-	-	-
1942	493.5	327.5	821.0
1943	472.6	494.4	967.1
1944	434.1	406.9	841.0
1945	749.3	562.9	1312.2
1946	475.8		475.8
1947	748.0	333.8	1081.8
1948	1169.8	832.3	2002.2
1949	2102.4	950.3	3052.7
1950	636.4	420.9	1057.3
1951	1823.4	676.3	2449.7
1952	369.2	527.1	896.3
1953	2040.7	438.2	2478.9
1954	1194.3	404.2	1598.5
1955	1181.6	629.1	1810.7
1956	865.0	463.6	1328.6
1957	2016.7	640.9	2657.6
1958	1165.3	735.3	1900.6
1959	1068.7	495.3	1564.0
1960	947.6	549.3	1496.9
1961	553.8	801.0	1354.9
1962	1124.5	907.2	2031.6
1963	1216.5	756.6	1973.1
1964	252.2	627.8	880.0
1965	381.0	647.3	1028.3
1966	237.2	751.6	988.8
1967	825.1	631.4	1456.5

[a/] From Lyle (1968) catches landed in ports of a given region

[b/] New England - Maine through Connecticut
Middle Atlantic - New York through North Carolina

Table 2

Historical Canadian squid (*Illex illecebrosus*), catches[a] in t, from ICNAF subareas 3[b] and 4, 1920-68 (Mercer, 1973)

Year	ICNAF Subarea 3	4	Total[2]
1920		449	449
1921		1118	1118
1922		605	605
1923		769	769
1924		343	343
1925		1012	1012
1926		1990	1990
1927		288	288
1928		415	415
1929		481	481
1930		596	596
1931		155	155
1932		118	118
1933		310	310
1934		62	62
1935		337	337
1936		423	423
1937		59	59
1938		113	113
1939		175	175
1940		243	243
1941		233	233
1942		28	28
1943		7	7
1944		48	48
1945		69	69
1946		394	394
1947		210	210
1948		41	41
1949		13	13

Year	ICNAF Subarea 3	4	Total
1950		139	139
1951		56	56
1952		97	97
1953		51	51
1954		115	115
1955	6815	269	7084
1956	7779	450	8229
1957	2593	335	2928
1958	718	84	802
1959	2853	258	3111
1960	5067	24	5091
1961	8968	50	9018
1962	481	587	1068
1963	2255	111	2366
1964	10400	346	10746
1965	7801	169	7970
1966	5017	102	5119
1967	6905	116	7021
1968	1	7	8

[a] Catches prior to 1938 were reported in barrels where 1 barrel is approximately 200 lb. Catches since 1938 were reported in '000s of lb, these were converted to t: 1 000 lb = 0.45359 t

[b] Catches from the Newfoundland area, ICNAF subarea 3, are not available prior to 1955, so these do not represent the total Canadian catch

Table 3

Squid catches (in t), by species[a], year and country, from the Northwest Atlantic: Cape Hatteras to the Gulf of Maine, 1963-78

	COUNTRY[b]															
Year	Bulg	Can	Cuba	Fra	FRG	GDR	Ire	Ita	Jap	Pol	Rom	Spa	USA	USSR	Mex[c]	Tot.
						Long-finned squid										
1963													1294			1294
1964													576	2		578
1965													709	99		808
1966													722	226		948
1967									5				547	1125		1677
1968									177				1084	2150		3411
1969									7125			438	899	1080		9542
1970									13250			2790	653	692		17385
1971	10								10426			3446	727	3560		18169
1972	20			288	463			2000	16293	164	66	5667	725	4048		29734
1973	46			793	1641			2360	14459	911	150	11148	1105	5000		37613
1974	172	27						3280	13493	1706	3	9375	2274	4520		34850
1975	34		30		27	16	1660	3390	10748	3785		7698	1621	4792		33801
1976	23		257		22	317	1042	3304	5029	1706	13	9137	3602	832		25284
1977	8	15	28			9		2237	7814	232		5236	1088	7		16674
1978								1366	2309		17	4603	1476	7	1053	10831
1979			-					2065	3099		14	4664	4433	9	3573	17857
1980			-					2241	6033	3		7569	4127			19974
						Short-finned squid										
1963													810			810
1964													358	2		360
1965													444	78		522
1966													452	118		570
1967									2				707	286		992
1968			10						1557				678	1026		3271
1969			1						586			128	562	260		1537
1970						20			389			1636	408	373		2826
1971	80	1							176			3324	455	2578		6614
1972	479		14	8				1200	2398	5264		4878	472	2928		17641
1973	364			27		313		805	1067	8288		3784	530	3977		19155
1974	420							980	3327	5003	6	6769	148	3975		20628
1975	171		121			882	3085	884	3237	3051	48	2204	107	4136		17926
1976		54	8		1101	996	2241	1117	3256	5050	9	4063	229	6812		24936
1977	52	5	6				23	1948	4876	656		8202	1024	8003		24795
1978								2131	3744	-	50	8583	385	33	2769	17695
1979							207	3070	3170	167		5594	1593		3540	17341
1980								2516	2410	282	55	8396	343	-	1230	15232

a/ 1963-66 estimated breakdown of total squid catch, prorated by ratio of reported *L. pealei* to *I. illecebrosus*, from ICNAF Statistical Bulletins No. 13-16
1967-76 from ICNAF Sum. Doc. 78/VI/6
1977-79 ICNAF Statistical Bulletins
1980 Preliminary, as reported to NMFS by foreign nations

b/ Countries are: Bulgaria, Canada, Cuba, France, Federal Republic of Germany, German Democratic Republic, Ireland, Italy, Japan, Poland, Romania, Spain, USA, USSR and Mexico

c/ Mexico did not fish in this area prior to US extended jurisdiction

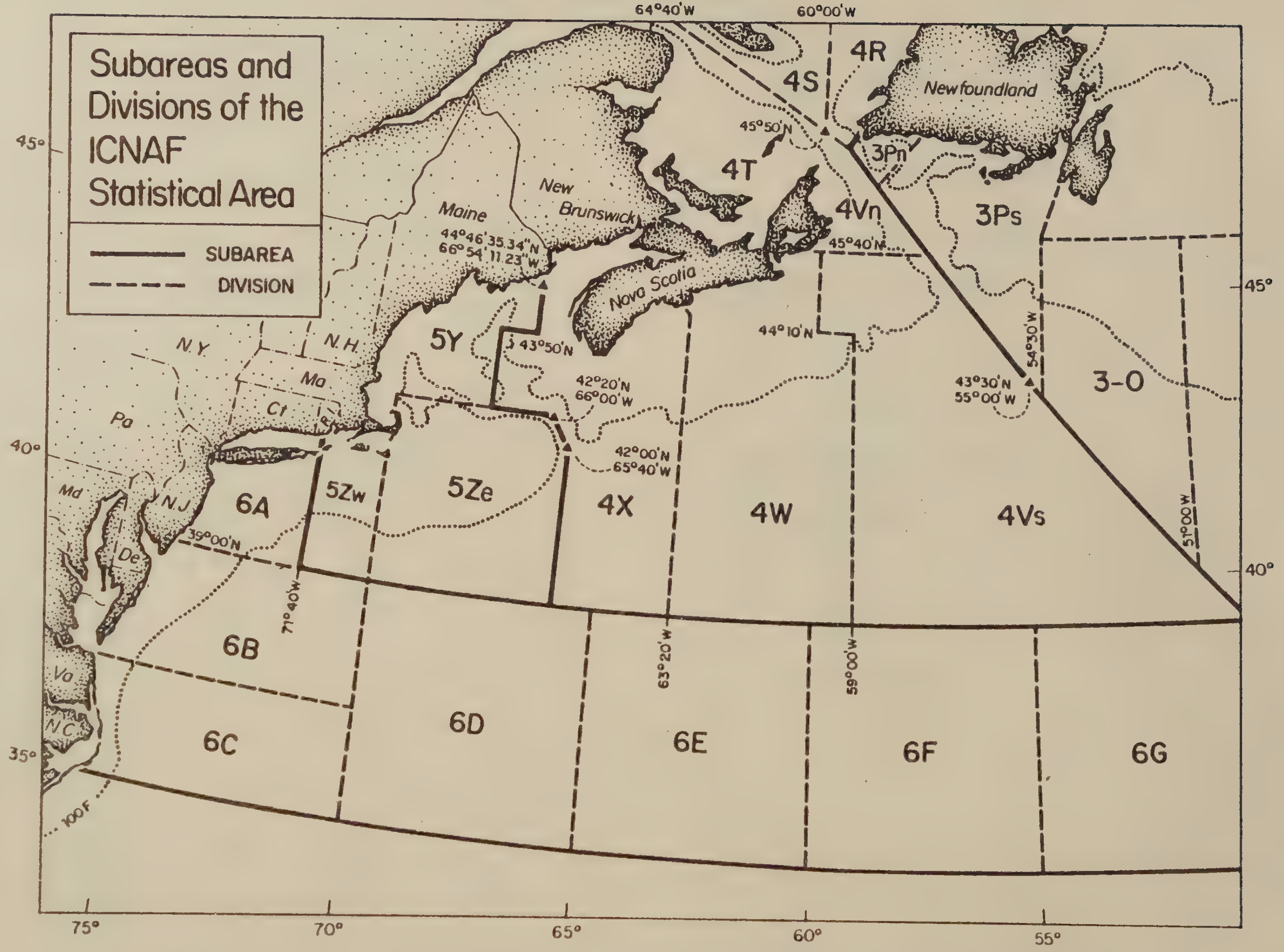

Subareas and Divisions of the ICNAF Statistical Area
SUBAREA
DIVISION
64°40'W
60°00'W
4R
4S
Newfoundland
45°50'N
4T
3Pn
3Ps
4Vn
New Brunswick
Maine
44°46'35.34"N
66°54'11.23"W
45°40'N
Nova Scotia
5Y
43°50'N
44°10'N
54°30'W
43°30'N
55°00'W
3-O
42°20'N
66°00'W
42°00'N
65°40'W
N.Y.
N.H.
Ma
Ct
Pa
Md
N.J.
De
Va
N.C.
6A
5Zw
5Ze
4X
4W
4Vs
39°00'N
71°40'W
63°20'W
59°00'W
51°00'W
6B
6C
6D
6E
6F
6G
100F
45°
40°
35°
75°
70°
65°
60°
55°

Figure 5 International Commission for the Northwest Atlantic Fisheries (ICNAF) subareas 3-5 and statistical area 6

The *L. pealei* fishery is centred in the southern New England-middle Atlantic area, from about Baltimore Canyon to the southwestern part of Georges Bank. This fishery occurs from November through March, while *L. pealei* is in its overwintering area, along the edge of the continental shelf (100-500 m). Most vessels participating in this fishery are sterntrawlers, ranging in size from 150 to 2 000 GRT (gross registered tons). The squid are generally frozen whole, in 10-20 kg blocks aboard the fishing vessels. Blocks are then transported to domestic markets by larger vessels.

The *I. illecebrosus* fishery takes place from about June through September, while this species has moved onto the continental shelf, although some short-finned squid are taken throughout the long-finned squid fishery. The major *I. illecebrosus* fishery off the USA has traditionally occurred from Hudson Canyon northeast to Corsair Canyon on Georges Bank, primarily by vessels which had participated in the winter, long-finned squid fishery. Off Canada, the fishery has concentrated along the shelf edge, primarily southeast of Nova Scotia.

Total annual catches for all countries (1963-80), of *L. pealei* and *I. illecebrosus*, from off the USA, and of *I. illecebrosus*, off Canada, are presented in Figure 6.

Management Under ICNAF

The International Commission for the Northwest Atlantic Fisheries (ICNAF), was established in 1950 as an international body designated for the task of management and regulation of the fishery resources of the Northwest Atlantic. ICNAF initiated management of Northwest Atlantic squid fisheries in 1974. A pre-emptive quota was established in response to the increase in catch by distant water fishing vessels from the initial 4 t reported by the USSR in 1964, to about 57 000 t in 1973. Most of the catch was off the USA (ICNAF SA 5 + 6; see Figure 6). Initial actions, based on a preliminary Japanese assessment of the *L. pealei* stock (Ikeda, Nagasaki and Imanaga, 1973), set the total allowable catch (TAC) of squid at 71 000 t in 1974 and again in 1975. In those two years 78 and 73 percent, respectively, of the TACs were taken. Beginning in 1976, separate TACs were established for each species in SA 5 + 6, and for *I. illecebrosus* in the Nova Scotia and Newfoundland areas (SA 3 + 4). Though no more than 64 percent of the entire squid TAC has been taken in SA 5 and 6, problems with reporting schemes resulted in the 1976 and 1977 SA 3 + 4 quotas (25 000 t each year) being surpassed by 167 percent and 323 percent, respectively.

Management Under Extended Jurisdictions

The US Fishery Conservation and Management Act (FCMA) of 1976, became effective on 1 March 1977. Since that time, the USA has withdrawn from ICNAF and assumed sole responsibility for management of the fishery resources within 200 mi of its land boundaries. A Fisheries Management Plan (FMP) with accompanying regulations went into effect immediately. Along with establishing standard requirements of reporting catch, and biological information, the squid FMP set the TAC for each species of squid (44 000 t for *L. pealei* and 30 000 t for *I. illecebrosus*), based on minimum biomass estimates and a model simulating the effect of fishing on these stocks (Sissenwine and Tibbetts, 1977). Fishing 'windows' (Figure 7), were established to regulate the foreign squid fisheries in time and place. These regulations remain in effect.

Canada also adopted a plan for extended jurisdiction, and in January 1977, began to manage and regulate all fisheries within 200 mi of its coast. In the Northwest Atlantic, however, Canada solicited the advice of ICNAF (and its successor, Northwest Atlantic Fisheries Organization, NAFO) in the management of stocks in its Fisheries Conservation Zone. In 1977 the TAC of 25 000 t, set by ICNAF for *I. illecebrosus*, was adopted. This TAC was also established for 1978, but at a special meeting of ICNAF's Standing Committee on Research and Statistics (STACRES), held in Cuba in February 1978 (ICNAF Sum. Doc. 78/VI/3), it was advised that this quota be raised to 100 000 t in ICNAF SA 3 + 4. Catches of *I. illecebrosus* in this area had increased steadily, from less than 10 000 t annually prior to 1975, to 80 000 t in 1977, with no apparent reduction in stock productivity. Biomass estimates presented at the STACRES meeting indicated that with an annual exploitation rate of 0.4 (though reasonable for this species, Sissenwine and Tibbetts, 1977) about 100 000 t could be removed in 1978. In 1978 a total of 98 700 t

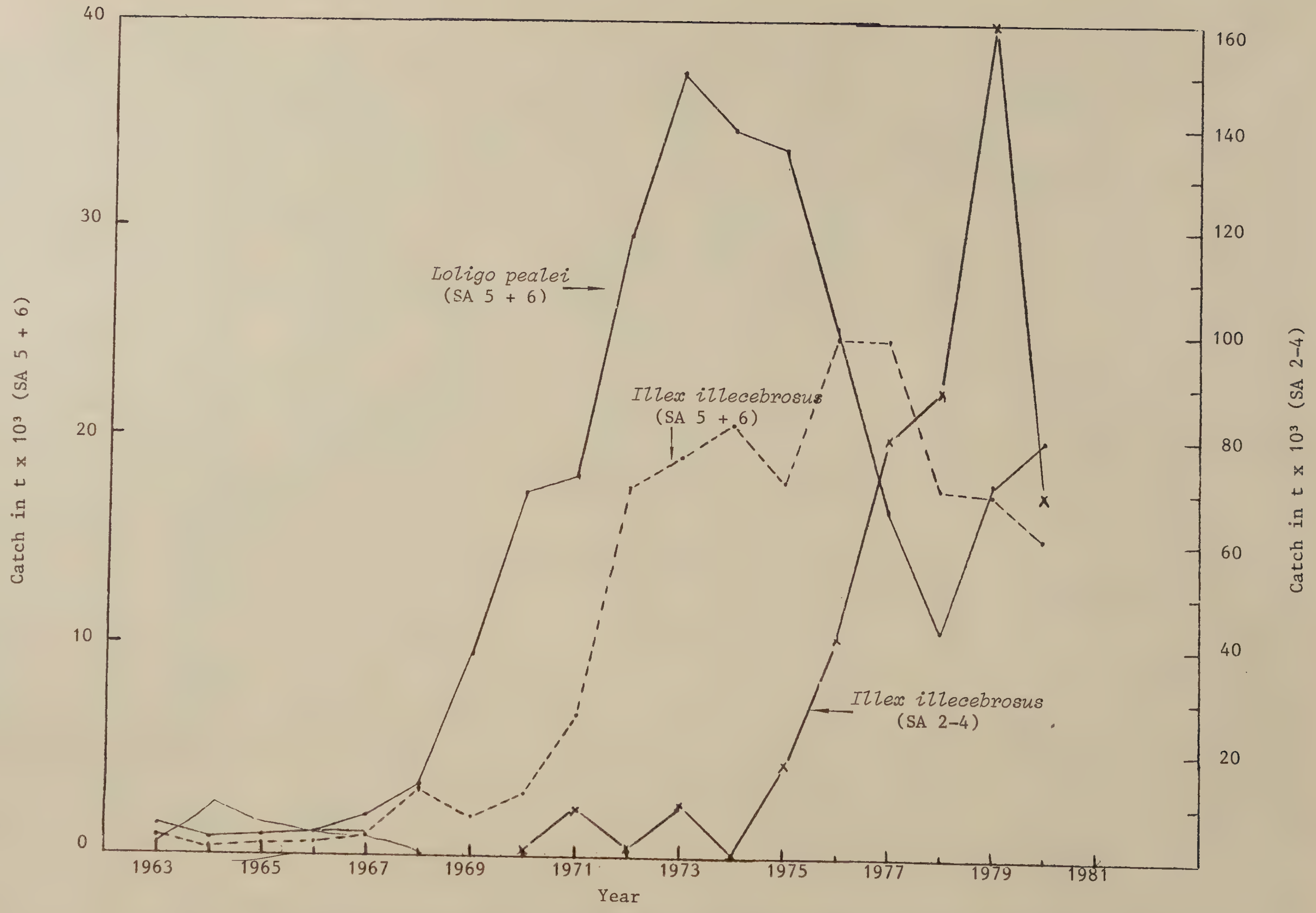


Figure 6 Total annual squid catches (*L. pealei* and *I. illecebrosus*) from ICNAF subareas 2-4 and subarea 5 and statistical area 6, all countries, 1963-80

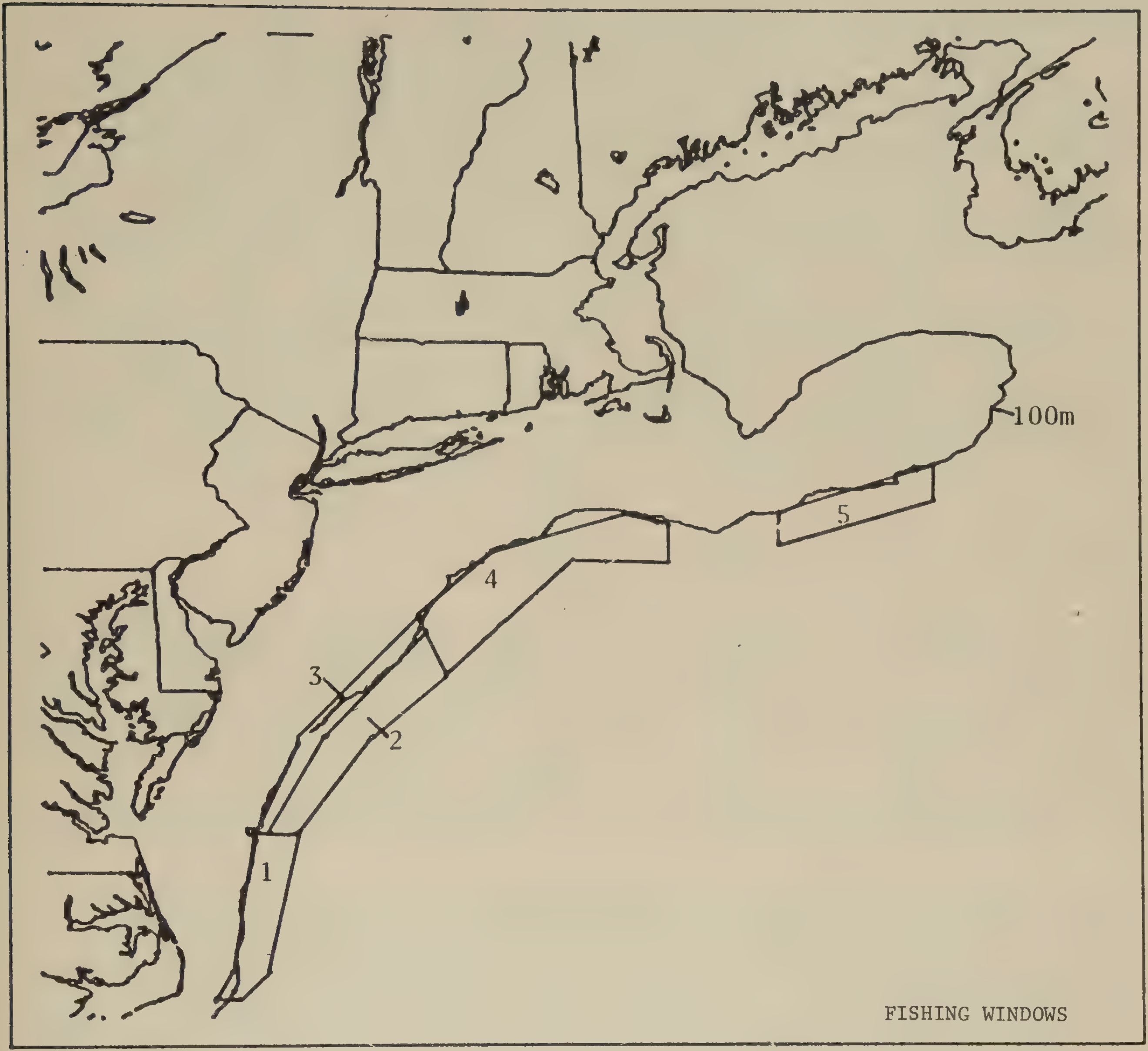


Figure 7 Areas of the Northwest Atlantic, off the USA, which are open to foreign fishing during authorized fishing seasons

were taken in SA 3 + 4, and in 1979 the TAC was again raised, this time to 120 000 t. The total catch from this area in 1979 was 162 000 t. The TAC was raised to 150 000 t for 1980-81. However, catches in 1980 totalled only 69 000 t. This dramatic reduction may be the result of market conditions and reduced effort.

Prior to establishment of extended jurisdiction by the USA and Canada, the short-finned squid had been managed as a single stock throughout its range. Separate quotas had been set in each of the areas off the USA and Canada, but this was to insure balanced levels of effort on the two stock components. Since 1977, however, with the dramatic increase in catches in SA 3 + 4, this balance does not exist, and until further knowledge of interaction of *I. illecebrosus* found off the USA and Canada is obtained, careful monitoring of the effects of the current levels of exploitation is necessary.

Life History and Growth

A protracted spawning season for *L. pealei* (April-October), produces a single year class, varying in age by as much as six months. However, modal analysis of length frequency distributions indicate that it may be appropriate to separate each year class into at least two distinct cohorts, in most years. Generally, these are late spring (April-June) and late summer (August-October) cohorts. These cohorts have been shown to have different growth rates, and based on growth schemes and mean sizes at maturity described for these cohorts (Lange, MS 1980), differences exist in age at spawning. Post-spawning mortality is assumed to be high for this species, so differences in age at spawning are significant.

Some individuals from the spring cohort mature over their first winter and begin spawning late in the summer of their second year (about 14-15 months at 18-22 cm), with the remainder of the cohort spawning during the following season (April-September; 22-23 months). Individuals of the late summer cohort are too small to mature during their first winter and do not begin to spawn until about April of their second year (18 months, at 22-25 cm). Although some individuals may survive to spawn at 35-37 cm in the following spring, most will spawn and die by October (about 24 months).

In most years it appears that the spring cohort is more significant than the late summer cohort, and that it contributes more to the fishery. The exact timing of hatching in any year may significantly alter this pattern.

Less is known of the maturation and spawning of *I. illecebrosus*, than of *L. pealei*, but it is assumed that they spawn in deep waters, off the edge of the shelf, between December and June. This, as with *L. pealei*, produces a single year class with as much as six months difference in age. Unlike *L. pealei*, the separation of year classes into more than one cohort is not apparent in every year, though remnants of more than one cohort are present in most months. Individuals spawned early in the season (December-January) have similar growth rates to those spawned later (May-June) However, differences in size between these groups result in differences in time of subsequent spawning and on the effects of fishing mortality through their life span. Therefore, separate cohorts are also assumed for this species.

Each cohort is assumed to mature and spawn at about 22-24 months, and 21-26 cm. The winter cohort is partially recruited to the offshore fishery in July of its first year (about 8 cm), and makes up a significant portion of the less important inshore fishery throughout the summer. This cohort is taken in the directed *L. pealei* fishery as it moves offshore in the autumn and winter, and makes up the major portion of the catch in the directed *I. illecebrosus* fishery during the following summer. The spring cohort is first susceptible to fishing as incidental catch in the winter *L. pealei* fishery (7-10 cm), and is fully recruited to the directed *I. illecebrosus* fishery in the summer (13-14 months, and 13-17 cm). This cohort is again taken, as it moves offshore, in the *L. pealei* fishery, until about April when it moves off the shelf to spawn. However, the winter cohort is presumed to comprise the major portion of each year class and, in fact, the proposed second cohort may not be apparent in some years, as the continuum of spawning is skewed toward the earlier months of the spawning season. This is particularly the case off Canada.

Sex and Maturity

Lange (MS 1980) found no significant difference in the overall sex ratio of *L. pealei* for data pooled over all years and months (1975-78) from US surveys. Individuals taken inshore during the late spring and summer when spawning occurs, contain a high proportion of mature individuals of both sexes, while most specimens taken in September through November were immature. The proportion of mature individuals of both sexes increases between March and April, and declines for offshore samples in May; while the proportion of mature individuals in the inshore samples is significantly greater. In September through November the influx of juveniles and the disappearance of large individuals result in dramatic reductions in the percent of mature individuals.

Lange (MS 1980) found that *I. illecebrosus* consistently exhibited a 1:1 sex ratio in the first part of the year (March-July), as this species moves onto the shelf from its offshore overwintering, or spawning grounds. However, by late summer, there appeared to be a distinct shift toward fewer males than females, which may be related to differences in rate of maturation. As males begin to mature before females (Durward, Amaratunga and O'Dor, 1979), they also begin to move offshore toward spawning grounds earlier than females, and would therefore be less available to the trawl survey.

Male *I. illecebrosus* were consistently found to be at a more advanced state of maturity than were females (Lange, MS 1980), in each month of the year and over months. Again, this may be attributed to the slower maturing process for males, which mature over several weeks or months, while females may progress through the final three stages of maturity in a matter of days (Yuri Froerman, pers. comm.; AtlantNIRO, USSR, 1978). However, these apparent differences in maturity between sexes may be an artifact of the maturity indices employed, such that visible changes in one sex may not be related to the comparably numbered stage of the other. In fact, more subtle changes in each sex may be well correlated, and maturation may follow the same time frame for each sex. In general, individuals were immature in the spring, with greater percents reaching maturity by summer, and with over 50 percent of the males ready to spawn by the time of the autumn surveys (September-November).

Age and Growth

A major difficulty in understanding the dynamics of *L. pealei* and *I. illecebrosus* stocks has been the lack of methods of age determination. Age at length is generally determined by: (a) observing changes in length over time from fish in captivity; (b) tagging studies, or (c) counting annuli laid down on hard body parts, such as scales or otoliths of fish, or on the shells of other molluscs. However, to date, none of these methods has proved suitable for squid. An alternative method of ageing is therefore needed.

A method of length-frequency modal analysis, based on the assumption of normal distributions of size within age groups, was used by Lange (MS 1980) to separate modal components of length frequences into adjacent parabolic shaped distributions representing age classes or cohorts.

Beginning with the smallest length mode, as the contribution of each successive component was calculated, it was subtracted from total frequency and the process applied to each subsequent residual mode. A FORTRAN computer programme, NORMSEP (normal distribution separator), designed by Hasselblad (1966) and modified by Tomlinson (1971), was utilized to calculate means and standard deviations for each mode. Length frequences were analysed separately by sex.

Length frequency data for southern New England was most extensive. Monthly summaries were prepared by pooling commercial fishery or research survey length-frequency samples from the southern New England area, by sex.

Mean lengths at age and standard deviations, calculated by NORMSEP, are presented in Tables 4 and 5. Time is relative to the number of months between each observed mean length, starting at time 1 for the first observation of a cohort. For both species, additional modes were identified in some months, but could not be correlated with other modes in adjacent months, so were not included. Lange (MS 1980) fit the von Bertalanffy growth model to the results from NORMSEP. The resulting parameter estimates and corresponding residual sums of squares are presented in Tables 6 and 7 for *L. pealei* and *I. illecebrosus*, respectively. There was generally more than one cohort of *L. pealei* present in each year, probably related to peaks in spawning, within a protracted (6-month) period. For *I. illecebrosus*, which is assumed to spawn between December and June, a single cohort was obvious in 1975, while two cohorts were apparent in both male and female samples in 1976.

For most cohorts, high residual sums of squares indicate that the von Bertalanffy model may not adequately fit the available age at length data, and may lead to unrealistic estimates (Gallucci and Quinn, 1979). This lack of fit may be associated with bias in mean lengths at age due to the differences in the sources of length data used in ageing.

Table 4

Mean length (cm) and standard deviations, at time (in months) for proposed cohorts of *L. pealei* from the southern New England area (1975-77), including data cohort was first observed

Cohort	Time	1 Length mean	Time	2 Length mean	Time	3 Length mean	Time	4 Length mean	Time	5 Length mean	Time	6 Length mean
Males date[a]	3/75		7/75		10/75		11/76		9/76		4/77	
	1	12.109 (2.621)	1	7.507 (1.610)	1	4.704 (1.224)	1	11.054 (1.754)	1	4.716 (2.005)	1	5.856 (1.336)
	3	13.920 (3.941)	3	7.314 (1.256)	7	7.047 (6.580)	6	18.031 (2.370)	3	7.723 (1.383)	2	7.840 (0.812)
	5	16.097 (3.683)	4	8.568 (1.753)	11	15.150 (2.688)	7	23.555 (2.551)	8	11.525 (1.356)	7	17.006 (2.592)
	6	16.037 (3.309)	5	8.599 (1.512)	13	16.955 (5.00)	12	26.310 (1.580)	9	16.643 (2.905)	9	21.631 (1.218)
	7	18.521 (4.195)	6	11.200 (1.845)	20	27.539 (1.920)						26.000 (3.43)
	10	24.101 (2.780)	8	12.290 (1.273)	21	29.850 (1.068)						
	12	23.490 (2.066)	9	12.290 (3.620)								
	13	23.000 (4.899)	11	13.800 (3.5)								
	15	23.300 (4.040)	13	17.150 (2.124)								
	18	23.910 (1.048)										
	20	25.610 (7.460)										
Females date[a]	3/75		3/75		10/75[b]		3/76		9/76			
	1	8.810 (2.32)	1	4.340 (0.805)	1	4.38 (.994)	1	5.170 (1.01)	1	5.640 (1.54)		
	3	9.220 (1.280)	5	6.500 (.733)	6	7.97 (1.34)	7	10.570 (2.91)	3	9.230 (2.07)		
	5	11.910 (2.21)	6	6.950 (1.02)	10	13.700 (1.61)	9	14.940 (3.94)	8	12.740 (1.00)		
	6	12.200 (.929)	8	8.880 (1.92)	12	17.460 (2.33)	14	16.740 (1.49)	15	21.40 (1.77)		
	8	15.340 (2.28)	9	8.870 (1.32)			15	16.030 (2.49)				
	9	14.190 (2.83)	10	12.530 (1.92)								
	10	17.500 (2.27)	12	14.490 (1.80)								
	12	19.550 (2.50)	13	14.570 (3.25)								
			17	18.300 (2.04)								

[a] Month when cohort was first observed in length frequency samples

[b] This cohort did not fit the von Bertalanffy model and is not represented in the table of parameters

Table 5

Mean length (cm) and standard deviations, at time (in months) for proposed cohorts of *I. illecebrosus* from the southern New England area (1975-77), including date cohort was first observed

Cohort	Time	1 Length Mean	Time	2 Length Mean	Time	3 Length Mean
Males date[a/]	10/75		9/76		9/76	
	1	10.225 (2.352)	1	14.355 (1.137)	1	7.893 (1.097)
	12	22.070 (1.376)	3	15.862 (1.650)	2	10.090 (1.276)
	14	26.009 (1.936)	4	15.980 (2.079)	3	9.970 (1.874)
	15	26.432 (2.111)	8	20.905 (1.528)	11	16.801 (1.508)
			11	21.776 (1.344)		
			12	22.219 (2.012)		
			14	23.435 (1.405)		
Females date[a/]	10/75		9/76		4/77	
	1	9.644 (2.259)	1	11.494 (1.834)	1	20.071 (1.938)
	12	17.897 (1.667)	2	11.432 (2.369)	11	21.031 (2.088)
	14	22.296 (1.131)	10	16.421 (0.500)	12	24.025 (1.595)
	15	21.543 (1.087)	11	16.833 (0.668)	14	26.316 (2.162)
			13	15.470 (2.065)		

[a/] Month when cohort was first observed in length frequency samples

Estimates of L_∞, which were well above (up to 25 times greater than) maximum lengths observed in nature, in 9 of the 16 cohorts (of either species), also indicate the model may not be appropriate for these species. However, squid are short-lived species which appear, in some instances, to grow continuously, throughout their lives. Determination of the appropriateness of this model should be modified to account for differences attributable to squid life history. Lange (MS 1980) fit alternative (linear and exponential) growth models to both species of squid.

Von Bertalanffy growth functions calculated for *I. illecebrosus* found off Canada, from 1977 to 1979 (Amaratunga, 1980), are:

Males $l_t = 2.39\ (1-e^{(-0.09(t-9.3))})$;

Females $l_t = 2.94\ (1-e^{(-0.054(t-6.8))})$

However, these functions were derived only from samples obtained while the species was inshore in the summer, and therefore do not reflect the effect of different growth rates in different seasons.

Table 6

Von Bertalanffy growth parameter estimates for *L. pealei* cohorts, by sex, including estimated date of hatching, range of observed ages (in months), and residual sums of squares

Cohort	Estimated date of hatching	L_∞ (cm)	K	t_o	Age Range (months)	SSR
Males						
1	10/74	27.921	.1016	-.0670	25	15.6563
2	12/74	461.280	.0018	-.0602	20	5.1082
3	8/75	1139.700	.0012	.0712	22	30.9618
4	5/76	42.173	.0630	-.0180	18	9.3075
5	6/76	209.560	.0065	-.3263	11	7.8964
6	11/76	348.34	.0062	2.2935	16	3.4591
Females						
1	9/74	110.260	.0108	-.4837	17	6.5147
2	12/74	613.450	.0016	-.7376	19	8.8050
4	11/75	24.451	.0650	.0195	18	5.1920
5	5/76	77.070	.01740	-.3822	18	2.6903

Table 7

Von Bertalanffy growth parameter estimates for *I. illecebrosus* cohorts, by sex, including estimated date of hatching, range of observed ages (in months) and residual sums of squares

Cohort	Estimated date of hatching	L_∞ (cm)	K	t_o	Age Range (Months)	SSR
Males						
1	2/75	548.700	.0023	-.1805	22	1.410
2	1/76	30.045	.0648	-.0607	21	1.863
3	3/76	36.253	.0383	-.1318	16	0.789
Females						
1	2/75	58.399	.0210	-.1998	22	4.110
2	1/76	18.198	.1194	-.0384	20	2.463
3	6/76	24.817	.1563	-.0376	23	12.242

Abundance and Biomass

Relative indices

The US research surveys, since 1967, have provided useful relative abundance indices by which *L. pealei* and *I. illecebrosus* abundance trends, from Maine to North Carolina may be monitored. Both species are distributed across the width of the shelf during autumn, while in spring, much of each population is still offshore (Figure 1 for *L. pealei* and Figure 2 for *I. illecebrosus*), so autumn survey catches are used to determine changes in relative abundance (and biomass) over years.

Canadian research surveys since 1970, also provided indices of *I. illecebrosus* in the areas around Nova Scotia and the Gulf of St. Lawrence (Koeller, 1980).

Minimum estimates

Minimum stock size estimates are obtained from areal expansion of stratified mean weight or number per tow, for each species.

Lange and Sissenwine (1980) describe minimum biomass estimates for squid based on US research vessel surveys. A first approximation of stock size, B_1, was made using the equation:

$$B_1 = WA/a$$

where: B_1 = estimate of biomass
W = stratified mean weight or number per tow
A = strata area sampled (in mi²)
a = area swept by each tow (0.011 mi² for US surveys)

Diel variations (caused by vertical migrations) in relative apparent abundance of *L. pealei* are significant, with daytime (08.00 to 16.00 h) survey catches 2.66 and 18.77 times greater (in weight and number, respectively), than night-time catches (20.00 to 04.00 h) according to Sissenwine and Bowman (1978). Therefore a second estimate (B_2) of *L. pealei* abundance was made by adjusting night catches upward when calculating stratified mean catch per tow, prior to areal expansion (Table 8). As diel variations in *I. illecebrosus* are not significant, no adjustments are made to the initial biomass estimate (B_1) for that species (Table 9).

It should be noted that the spatial distribution of *I. illecebrosus* further offshore is unknown. Consequently, the abundance indices observed in the survey areas may reflect yearly distributional differences in these areas for this species, and not overall population size. Also, catchability, or the portion of the stock taken by a single tow, for *I. illecebrosus* may be somewhat less than for *L. pealei*, due to the differences in vertical distribution through the water column, or a greater ability to escape the passing trawl.

Estimates of *I. illecebrosus* biomass, made by the USSR, ranged from 58 000 to 258 000 t, between 1971 and 1976. However, these estimates were for the Georges Bank and Nova Scotia areas (Konstantinov and Noskov, 1977).

Estimates of *I. illecebrosus* biomass from the Scotian Shelf and the Gulf of St. Lawrence (Koeller, 1980), from 1970 to 1979, ranged from 1 900 to 203 700 t and from 0 to 30 830 t, respectively (Table 9). The estimates for the Scotian Shelf followed the same general trends as those for the Cape Hatteras to Gulf of Maine areas, with peak biomass (203 700 t) estimated in 1976 and with relatively high levels in 1979 (70 300 t) and 1977 (46 600 t). Estimates of biomass from the Gulf of St. Lawrence are sporadic, with values of 0 and 50 or less tons in four of the nine years where estimates are given. However, biomass since 1976 has been substantially greater than in earlier years.

Table 8

Loligo pealei minimum biomass (in t) and abundance (in number x 10^6) estimates, 1968-80 (from Lange and Sissenwine 1980, with 1979-80 updates)

YEAR	B_1MT WEIGHT	B_1 # x 10^6	B_2MT WEIGHT	B_2 # x 10^6
1968	28,073	692.6	29,114	1,211.9
1969	37,643	931.6	48,053	2,393.1
1970	12,095	337.9	19,640	1,946.2
1971	11,752	641.4	14,050	1,106.1
1972	25,400	1,065.1	21,039	1,533.3
1973	42,338	1,460.9	44,252	3,092.0
1974	32,014	989.0	46,442	4,757.0
1975	41,912	2,412.0	48,636	7,789.0
1976	44,935	1,632.0	51,436	4,372.0
1977	31,600	1,526.0	27,421	3,157.0
1978	16,583	556.0	18,800	1,251.0
1979	14,741	760.9	19,333	2,113.6
1980	31,130	1,436.7	50,523	9,313.5

Table 9

Illex illecebrosus minimum biomass (in t) and abundance (in numbers x 10^6) estimates, 1968-80 from the mid-Atlantic to the Gulf of St. Lawrence, by area

	Mid-Atlantic - Gulf of Maine[a]		Scotian Shelf[b]	Gulf of St. Lawrence[b]
YEAR	Biomass (MT)	Abundance (No. x 10^6)	Biomass (MT)	Biomass (MT)
1968	1,845.4	9.7		--
1969	418.8	3.6	--	--
1970	1,523.6	14.6	1,900	0
1971	2,024.1	10.1	14,700	360
1972	1,716.1	15.0	3,200	20
1973	1,862.0	8.2	8,900	50
1974	2,500.0	18.1	9,500	0
1975	8,306.0	60.3	24,800	1,000
1976	42,929.0	134.3	203,700	16,930
1977	21,747.0	73.3	46,600	15,270
1978	26,435	120.7	11,200	30,830
1979	41,455	144.2	70,300	--
1980	18,729	80.1	--	--

[a] Lange and Sissenwine, 1980 (1979-80, updated)
[b] Koeller, 1980

Pre-Recruit Abundance

L. pealei and *I. illecebrosus* in commercial length samples are usually greater than 8-10 cm in mantle length, respectively. Therefore, the abundance of individuals less than or equal to the appropriate length at recruitment, in autumn bottom trawl survey catches, is a useful pre-recruit index (Table 10).

Table 10

Pre-recruit and total abundance indices for squid, *L. pealei* and *I. illecebrosus*, 1967-80

	L. pealei		*I. illecebrosus*	
YEAR	Pre-recruits	Total	Pre-recruits	Total
1967	126.9	134.5	0.7	2.1
1968	159.9	176.5	0.6	2.3
1969	217.4	237.3	0.3	0.8
1970	79.3	85.6	0.2	3.4
1971	161.5	163.3	0.6	1.9
1972	258.5	271.4	1.8	3.5
1973	353.9	372.0	0.3	1.3
1974	233.3	251.7	2.1	3.0
1975	593.3	614.4	9.6	12.4
1976	302.5	410.9	0.6	28.7
1977	297.7	388.5	1.1	15.8
1978	9.34	144.2	5.1	28.4
1979	156.5	193.7	2.6	32.1
1980	279.8	364.1	0.7	17.0
1981	161.8	226.2	0.5	54.8

For *L. pealei*, most of the catch in numbers during the US autumn surveys are pre-recruits, but these are much less important to survey catch in weight. Even though these *L. pealei* pre-recruits are the mainstay of the winter offshore fishery there has been no significant correlation between these indices and subsequent catches or catch per effort in the commercial fishery, or in subsequent survey catches.

I. illecebrosus pre-recruits are rare in US survey catches, and are not taken by Canadian Surveys, but when they are abundant to the US survey as a result of significant late spring or summer spawning, they may be a good predictor of the following summer's fishery (note 1975, 1978 and 1979). It should also be noted that when *I. illecebrosus* pre-recruits are scarce it may be due to distributional differences and the abundance during the following summer may still be high.

ANALYSIS OF EXPLOITATION AND MANAGEMENT ALTERNATIVES

Several models have been proposed to describe the effects of fishing on the stocks of *L. pealei* and *I. illecebrosus* to the Northwest Atlantic. Sissenwine and Tibbetts (1977), Caddy (1979), and Hurley and Mohn (1979), presented models which incorporated factors such as spawning mortality, immigration and emigration, and cohort structure into the Ricker yield per recruit model. Kawahara (1979) developed yield per recruit models based on the method of Thompson and Bell (1934), while considering the effects of migration. Since the stock recruitment relationship for these species is not known, most of the simulations presented by these authors have been based on single year classes, assuming a constant average level of recruitment. However, Sissenwine and Tibbetts (1977) did assume a Beverton-Holt stock recruitment relationship and extended yield per recruit analyses to estimate equilibrium yield from each stock, at several levels of exploitation.

Many of these models were limited in that they did not include concepts of a protracted spawning season or of multiple cohorts, or they did not cover the areas considered here. Two more recent models relevant to current management, are those by Lange (in press) and Mohn (1981). These are reviewed below.

Multiple Cohort Yield Model for Squid Off the Northeast Coast of the USA (Lange, in press)

A modified Ricker (1958) yield model incorporating information about proposed cohorts was developed. Let NO be the number of squid from both cohorts, in the initial population, and PN1 the proportion of the initial population from cohort I (therefore (1-PN1) is the proportion of cohort II). For each cohort, during any time period (t), N is the number of squid in the cohort, W the average weight of an individual in that cohort, YN the catch in numbers, and Y the catch in weight from the cohort. Then:

$$N_0 = \text{NO} \times \text{PN1 for cohort I } (= \text{NO}(1-\text{PN1}) \text{ for cohort II})$$

$$N_t = N_0 e^{-(F+M+S)t}$$

$$W_t = W_0 e^{gt}$$

$$YN = FN_0(1-e^{-(F+M+S)t})/F+M+S$$

$$Y = FN_0W_0\ (1-e^{-(F+M+S-g)t})/F+M+S-g$$

where F, M, S and g are instantaneous average monthly fishing mortality, natural mortality, spawning mortality and growth rates for the appropriate cohort during time t. N_0 and W_0 are initial conditions for the given time period, for the cohort.

The sum of the number of individuals in both cohorts at the time, in months, when the first cohort is recruited, was assumed to be 1 000 for the virgin stock, although the portion of this number associated with the second cohort will not actually be present until the time of hatching (t+a delay time, in months). Equations were then applied to each cohort on a monthly basis, with F, M, S and g assumed constant within month, through the proposed life span of the year class. Monthly results from the two cohorts were then summed to provide monthly values of stock size and yield in weight and number.

The total yield per 1 000 recruits summed over all months of the life span was calculated for combinations of M and F-multipliers as described for each species. The effects of annual differences in time of spawning were examined by varying the cohort structure, represented by the proportion of the year class which was assumed to be from each cohort.

Assuming *L. pealei* has a mesh selection factor similar to that found by Ikeda et al. (1973) for *Loligo* sp. in the Eastern Central Atlantic (1.92), these cohorts are also subjected to different rates of fishing mortality. A retention of 50 percent (at 8.6 cm with the 45 mm mesh currently used in the fishery) occurs in November for the spring hatched cohort and during the following March for the summer cohort.

Instantaneous monthly average growth rates were calculated for each cohort based on Lange's (1980) estimates of length at age and length-weight functions (Lange and Johnson, 1981).

$$G_t = \log_e (W_{(t+1)}/W_t)$$

Initial weights (W_0) for cohorts I and II were assumed to be 0.349 and 0.664 g, respectively.

Spawning rates (S) were chosen such that for the unexploited fishery the number spawning in the second season would be 60 percent of those spawning during the first season for cohort I (hatched April-June) and 10 percent for cohort II (hatched August-October). The choice of these percents was based on the ratio of percent frequencies, from 1973 to 1979 survey cruise lengths frequency data, of spawning sized individuals, for each cohort, during their first and second spawning seasons (i.e., for cohort I, the percent of 29-33 cm individuals in spring: the percent of 18-24 cm individuals in autumn surveys). Within the first season, for each cohort, spawning rates were set such that the ratio of spawned to non-spawned individuals at the end of each month of the spawning season was nearly constant, since analyses indicate constant percents of mature individuals through the spawning season. All individuals are assumed to perish by the end of the second spawning season.

Several choices of monthly natural mortality rate (M), held constant over the life span of each cohort, were used in this analysis. These were based on a wide range of assumptions of life expectancy which produced effective monthly Ms ranging from 0.01 to 0.15 (M = 1/T, where T = life expectancy, in months).

The seasonal nature of the *L. pealei* fishery is represented by estimates of relative monthly fishing mortality rates (F_r). Each monthly value is the ratio of the catch for that month (average from the 1977-79 fisheries) to the catch from the month with the greatest average catch (February). These relative Fs are used in conjunction with a range of F-multipliers (Paulik and Bayliff, 1967) held constant over the life span and representing several assumptions of instantaneous fishing mortality rates, to reflect changes in fishing effort over the fishing year. The F-multipliers used ranged from 0.05 to 0.50. The relative Fs were reduced in months prior to full recruitment, based on approximated selection curves, to reflect the effects of mesh selection on retention of different size *L. pealei*.

Instantaneous growth rates (g) for each hypothetical *I. illecebrosus* cohort were estimated as described for *L. pealei*, with initial weights of (W_0) 0.283 and 0.269 g. Spawning rates were chosen for each cohort such that an equal number of individuals in the unexploited fishery would spawn in each month of the spawning season of that cohort. These spawning rates are equivalent to spawning mortality rates since it is assumed that individuals die after spawning.

Estimates of monthly natural mortality (M) ranging from 0.01 to 0.10, assumed reasonable for the life expectancy of this species (as described for *L. pealei*), were used in this analysis. M was held constant through the life of the cohort.

Monthly values of relative fishery mortality (F_r) were calculated as for *L. pealei* and applied in the model to reflect the seasonality of the fishery. Multipliers of F, ranging from 0.05 to 1.5 were used to simulate a variety of possible monthly fishing mortality rates.

Results

The simulated yield per recruit of *L. pealei* in weight (kg) per 1 000 individuals recruited to the fishery, is plotted (Figure 8) against F-multipliers (FM) ranging from 0.05 to 0.5, for monthly M values of 0.01, 0.03, 0.08 and 0.15 and assuming PN1 = 0.75. This cohort ratio reflects the observation that in most years the spring cohort is more significant than the late summer cohort. The results were similar for other realistic assumptions of cohort structure at high levels of M (0.15), but for lower M values, higher yields per recruit were obtained when significant portions (≧ 25 percent) of the

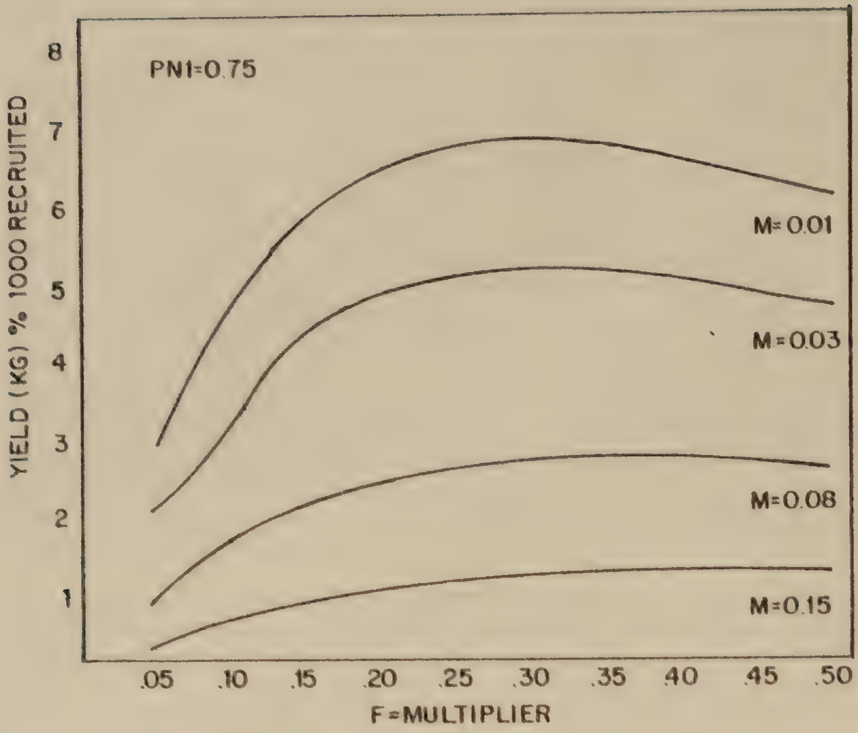


Figure 8 Yield per 1 000 recruits for *I. pealei* for M = 0.01, 0.03, 0.08 and 0.15; when 75 percent of the year class is assumed from the spring cohort

year class were assumed to be from the second cohort (PN1 < 0.75). This seems reasonable since if major spawning occurs later in the spawning season as happens in some years, fewer individuals from a year class are susceptible to the winter-directed fishery. Maximum yields per recruit generally occurred at FM = 0.3 for M = 0.01 and 0.03, and at higher FMs (0.35 to 0.5) when M was assumed to be higher.

The simulated yield in weight (kg) per 1 000 *I. illecebrosus* recruited to the fishery is plotted against FM (ranging from 0.05 to 1.5) for M values of 0.01, 0.04 and 0.1; assuming PN1 = 0.80 (Figure 9). The results were similar for other values of PN1. Maximum yield per recruit occurs at FM of 0.4 for M = 0.01 and 0.04 and at FM = 0.5 for M = 0.1.

Yield per Recruit Analyses and Management

The results of the yield per recruit analyses discussed thus far were based on the effects of the 1977-79 squid fishery, which primarily employed 45 mm mesh nets. However, increases in the mesh size and therefore age at entry in the directed fisheries of both *I. pealei* and *I. illecebrosus* will effect yield per recruit. Potential effects on yield per recruit in these fisheries, of changing mesh regulations to 60 mm and to 90 mm, were also simulated by Lange (1980).

All population parameters were assumed to be as described for the present fisheries of *I. pealei* and *I. illecebrosus*. The relative monthly fishing mortality rates (F_r) in the months when each cohort first enters the fishery were based on mesh selection information, and reflect changes in age at entry from increases in mesh size.

Yield, in weight per recruit, estimates for *I. pealei* for both the 60 and 90 mm meshes were consistently greater than for the 45 mm mesh for all choices of M and F-multipliers (Figure 10). However, yield of *I. pealei* appears to be more sensitive to changes in natural mortality than to mesh selection. Although size at entry (caused by mesh selectivity) is an important factor in potential yields at low levels of M, this factor becomes less important when M is large (0.15).

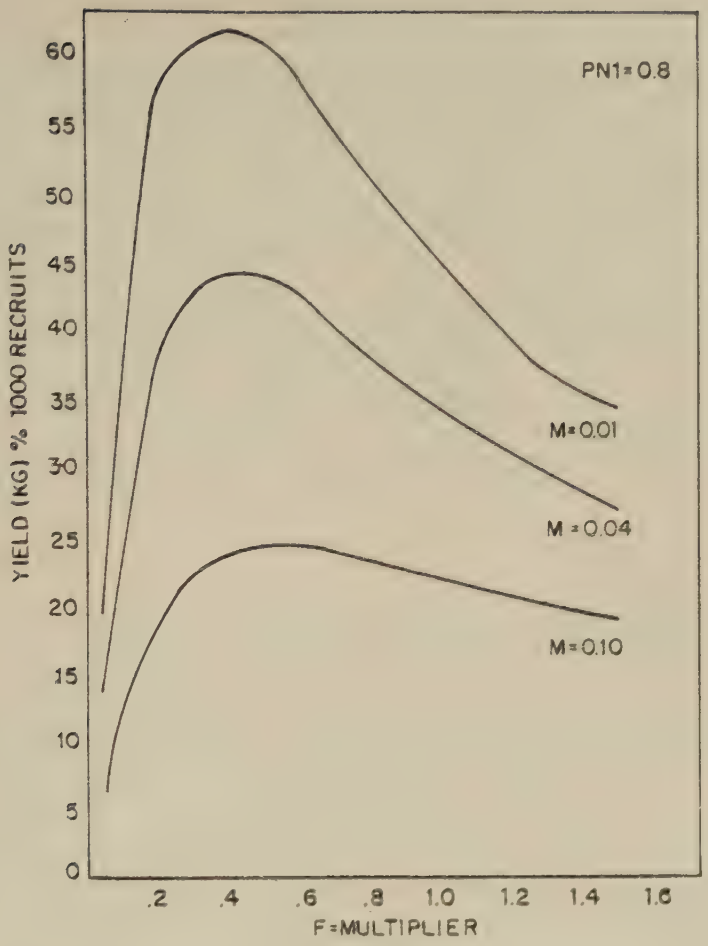


Figure 9 Yield per 1 000 recruits for *I. illecebrosus* for M = 0.01, 0.04 and 0.10; when 80 percent of the year class is assumed from the winter cohort

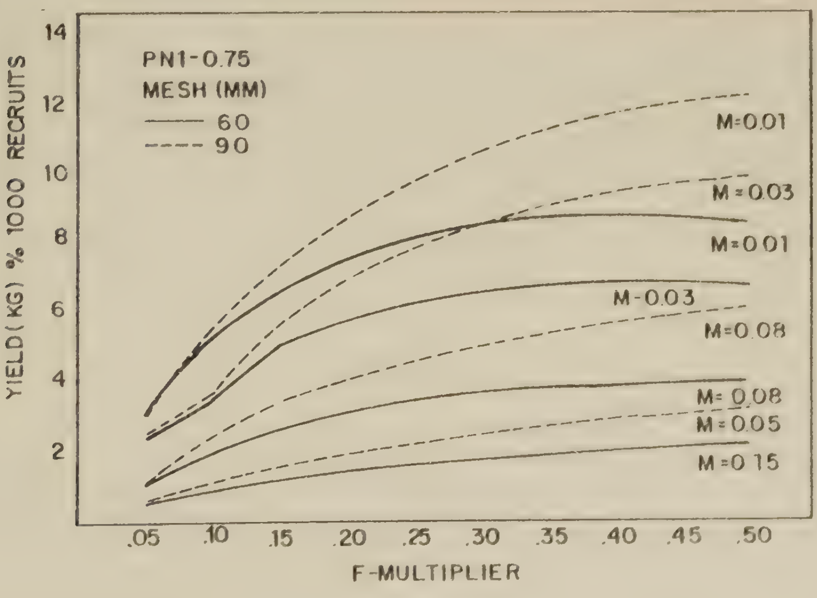


Figure 10 Yield (kg) per 1 000 recruits for M = 0.01, 0.04 and 0.15; and for mesh sizes of 60 and 90 mm, assuming that 75 percent of the year class is from the spring cohort

Simulated yield per recruit for *I. illecebrosus* was well above that expected in the present fishery (45 mm mesh), for both 60 and 90 mm meshes, over the entire range of F-multipliers (Figure 10). In all cases, estimated yield was greater for 90 mm than for 60 mm mesh, as well. Significant increases in yield in weight per recruit, of both *L. pealei* and *I. illecebrosus* may result from increases in size at entry into the fishery, as would occur with increase in mesh size.

Yield per Recruit for *I. illecebrosus* on the Scotian Shelf (from Mohn, 1981)

This model simulates the life cycle of *I. illecebrosus* from recruitment on the shelf. The yield per recruit model is an extension of the method of Thompson and Bell (Ricker, 1975). Factors controlling yield were temperature, choice of cannibalism model and the intensity and pattern of fishing. One million recruits were assumed to enter the fishery on 1 April, and simulation was followed for 21, two-week periods. The basic model is:

$$C = FN(1-e^{-(MC+MM+MN+F)})/(MC+MM+MN+F)$$

where F = fishing mortality
MC = cannibalism mortality
MM = migration mortality
MN = natural mortality
N = initial number of individuals at the start of the period
C = catch in number for the period

Growth was assumed to be represented by the von Bertalanffy function, with parameters as presented by Amaratunga (1980) for 1977-79. In the model, growth is also constrained between 5 and 7°C. Weight at age was calculated with a length-weight function.

Offshore migration of this species is related to the onset of stage 3 of migration, leading to spawning. A sigmoid curve, the integral of a normal distribution, with mean on 1 December and a standard deviation of 1 period (two weeks), was assumed as a first approximation to emigration. Therefore, the emigration rate is half its maximum on 1 December. The maximum instantaneous emigration rate was assumed to be 0.2, after incorporating a factor for cannibalism into the value of 0.31 derived by Hurley and Peck (1979). Migration was assumed to be proportional to abundance, and was treated as a mortality because it removes animals from the fishable population without contributing to the catch.

Cannibalism was assumed to be a significant contributor to the natural mortality of *I. illecebrosus* during its residency on the shelf. Mohn used two approaches to estimate the effects of cannibalism, including the relationships of efficiency of food utilization to growth, and of feeding frequency to growth. Data for percentage of squid in stomach contents throughout the season (Amaratunga, 1980; Ennis and Collins, 1978), were converted to mortality rates according to these two approaches.

Mohn defined the following relationship to estimate mortality by cannibalism (MC) over a period:

$$MC = \ln(K\bar{W}E/K\bar{W}E + \Delta WH)$$

where K = ratio of prey weight to predator weight
W = average prey weight
E = efficiency of food conversion
ΔW = weight gain of the predator
H = the percentage of squid in stomach

The value for the conversion efficiency (E) was set at 0.25 throughout the simulation, and K was assumed to be constant at 0.20, therefore:

$$MC = \ln(0.05\bar{W}/0.05\bar{W} + \Delta WH)$$

The second approach, though mathematically simpler, requires estimates for the animals feeding rate. Mortality due to cannibalism was simulated over a two-week time step, as:

$$MC = NFP \ln(1+H)$$

where NFP = number of feeding periods for the time step
H = percentage of squid in the stomach, as a function of size

In his simulation, Mohn chose a maximum value of five feeding periods at the beginning of the season and reduced these to three by the following January. The feeding rate was also assumed to drop throughout the season. Mortalitites generated by the second approach were generally higher than those for the food conversion approach.

Natural mortality was estimated to be 0.06 per two-week period, based on an assumed life span of one year, and was held constant throughout the simulation.

Relative fishing mortality rates were estimated based on the average pattern for the 1977-79 international fleet, fishing in SA 4 (Amaratunga, in press), combined with the selectivity pattern for 60 mm mesh trawls (Amaratunga *et al.*, 1979). The ogive for this mesh was approximated to a 50 percent retention of 122 mm with a standard deviation of 33 mm.

Results

The simulated yield (kg) of *I. illecebrosus* per 1 million recruits entering the fishery, for two assumptions each of bottom temperature, and method of cannibalism, and assuming three possibilities of time of onset of fishing and five levels of fishing mortality (F) are presented in Table 11 (Mohn, 1981). For all cases of temperature and cannibalism type, yield per recruit increased with increased F and earlier onset of fishing. This indicates the importance of the effects of natural mortality, and therefore cannibalism (which makes up over 60 percent of the total natural mortality), on *I. illecebrosus* while it is on the shelf. However, Mohn found that the sum of the three mortalities he presented exceeded the slopes of the log of the commercial catch per effort, over the fishing season. This indicates that either there were errors in the model, or that the stock exploited by the offshore fleet on the Scotian Shelf is not closed with respect to recruitment. If recruitment occurs over a relatively long period, catch per effort would remain high compared to model predictions. The model also predicts a faster rate of decline in abundance during the warmer years, as was evidenced in 1977 and 1979 (considered to be warm compared to 1978).

Yield per Recruit Analysis and Management

The results of the yield per recruit analysis for *I. illecebrosus* on the Scotian Shelf indicate that increased yield would result from increasing effort and an earlier onset of the fishery (within the levels described by the simulation). There was approximately a 50-170 percent increase, depending upon the assumptions applied, in the predicted yield per recruit if fishing commenced at the beginning of week 28 (1 July) as opposed to week 32 (1 August). This increase was magnified with increased bottom temperatures.

This model indicates that yield per recruit would be less in the warm years although this effect may be masked by the greater levels of recruitment which may occur during those warmer years.

CONCLUSION

Northwest Atlantic squid fisheries, fisheries management and supporting fisheries research are recent developments. It is already clear that squid resources of the region can support substantial (more than 100 000 t) although highly variable, fisheries. A year-round fishery is feasible off the northeast coast of the USA if vessels are suitable for fishing at the edge of the continental shelf during winter.

The population biology of *L. pealei* and *I. illecebrosus* is unique with respect to most exploited species of the Northwest Atlantic. Their lifespan is short, probably one or two years. There are multiple cohorts, of varying relative importance, each year. Squid probably sustain a high post spawning mortality. They lack scales or otoliths, therefore age determination is difficult. They are fragile and difficult to study in captivity. The entire range and migratory behaviour of *I. illecebrosus* is unknown.

Table 11

Yield per recruit analyses (kg/million recruits)

Bottom temperature	5.8°			6.5°			6.5°		
Cannibalism estimate type	"efficiency"			"efficiency"			"frequency"		
Onset (week)	24	28	32	24	28	32	24	28	32
F									
.02	1336	1144	686	867	715	414	564	386	140
.05	3131	2683	1625	2037	1678	980	1361	928	338
.10	5654	4851	2986	3695	3037	1798	2571	1745	640
.20	9403	8070	5100	6205	5072	3064	4631	3114	1157
.40	13888	11867	7762	9344	7523	4652	7742	5107	1933

In spite of these obstacles, much progress has been made toward understanding the population dynamics of squid. The life cycle of both species has been described. Based on modal analysis of length frequencies, their growth has been modelled by a variety of functions including von Bertalanffy. Trends in abundance and recruitment are monitored by research vessel bottom trawl surveys. Yield per recruit models have been adapted to take account of unique characteristics of squid.

Northwest Atlantic squid resources are regulated by catch quotas. Recent yield per recruit models indicate that yield could be increased by altering the seasonal pattern of fishing and increasing the minimum size of capture.

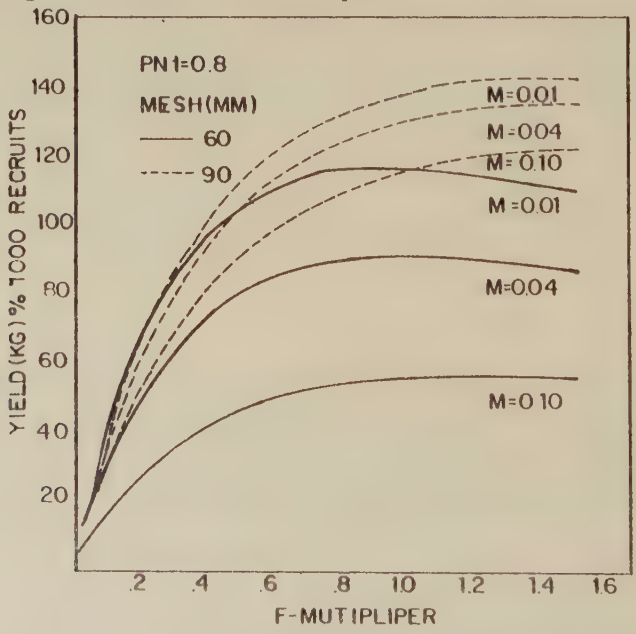


Figure 11 Yield (kg) per 1 000 recruits for M = 0.01, 0.04 and 0.10, and for mesh sizes of 60 and 90 mm, assuming that 80 percent of the year class is from the winter cohort

REFERENCES

Amaratunga, T., Growth and maturation patterns of the short-finned squid *Illex*
1980 *illecebrosus* on the Scotian Shelf. NAFO SCR Doc. 80/II/30, Ser. No. N062:17 p.

___________, The short-finned squid *Illex illecebrosus* fishery in eastern Canada.
J.Shellfish Res., 1(2) (in press)

Amaratunga, T., *et al.*, Food and feeding of the short-finned squid *Illex illecebrosus*,
1979 on the Scotian Shelf in 1978. ICNAF Res. Doc. 79/III/11, Ser. No. 5336:24 p.

Caddy, J.F., Preliminary analysis of mortality, immigration and emigration of *Illex*
1979 populations on the Scotian Shelf. ICNAF Res. Doc. No. 79/VI/120, Ser. No.
8488:21 p.

Dawe, E.G., P.C. Beck and H.J. Drew, Distribution and biological characteristics of
1981 young short-finned squid (*Illex illecebrosus*) in the Northwest Atlantic,
February 20-March 11, 1981. NAFO SCR Doc. 81/VI/23, Ser. No. N302:20 p.

Durward, R.D., T. Amaratunga and R.K. O'Dor, Maturation index and fecundity for female
1979 squid, *Illex illecebrosus* (LeSueur, 1821). Res.Bull.ICNAF, (14):67-72

Ennis, G.P. and P.W. Collins, Food and feeding of the short-finned squid, *Illex*
1978 *illecebrosus*, during its seasonal occurrence in the Newfoundland area.
Sel.Pap.ICNAF, 5:25-9

Gallucci, V.F. and T.J. Quinn III, Reparameterizing, fitting and testing a sample growth
1979 model. Trans.Am.Fish.Soc., 108(1):14-25

Hasselblad, V., Estimation of parameters for a mixture of normal distribution. Technometrics,
1966 8(3):431-44

Hurley, G.V. and P. Peck, Assessment of the short-finned squid, *Illex illecebrosus*, in
1979 the ICNAF Subarea 3 for 1978. ICNAF Res. Doc. 79/II/25, (Rev.) Ser. No. 5351

Hurley, G.V. and R.K. Mohn, Considerations on the management of the international squid
1979 (*Illex*) fishery in ICNAF Subarea 4. ICNAF Res. Doc. 79/II/24, Ser. No.
5350:11 p.

Ichikawa, W. and T. Sato, Development of *Illex illecebrosus* (LeSueur) fishing in the
1975 Northwest Atlantic - off New York to Newfoundland. Sekai No Ika-Tako Shigen
No Kaihatsu To Sono Riyo (Inf.Ser.Jap.Mar.Resour.Res.Cent.), (5):155-63.
Issued also as Transl.Ser.Fish.Mar.Serv.Can., (4105)

Ikeda, K., F. Nagasaki and H. Imanaga, Stock assessment of common American squid in
1973 ICNAF Subarea 5 and Statistical Area 6. ICNAF Redbook, 1973 (3):145-7

___________, Volume of common American squid, *Loligo pealei*, by trawl fishing in the
1975 waters controlled by ICNAF in the Atlantic Ocean and the volume of resources.
Sekai No Ika-Tako Shigen No Kaihatsu To Sono Riyo (Inf.Ser.Jap.Mar.Resour.
Res.Cent.), (5):1109-72. Issued also as Transl.Ser.Mar.Fish.Serv.Can., (4107)

Kawahara, S., Optimum rate of exploitation and virtual population analysis for short-
1979 finned squid, *Illex illecebrosus*, in Subareas 3 and 4. ICNAF Res. Doc.
79/II/21, Ser. No. 5347:10 p.

Koeller, P.A., Distribution, biomass and length frequencies of squid (*Illex illecebrosus*)
1980 in Divisions 4TVWX from Canadian research vessel surveys: an update for 1979.
NAFO SCR Doc. 80/II/17, Ser. No. N049:11 p.

Konstantinov, K.G. and A.S. Noskov, Report on the USSR investigations in the ICNAF area,
1977 1976. Annual meeting. ICNAF, 1977. ICNAF Summ. Doc. 77/VI/15, Ser. No.
5071:39 p.

Lange, A.M.T., The biology and population dynamics of the squids, *Loligo pealei* (LeSueur)
1980 and *Illex illecebrosus* (LeSueur), from the Northwest Atlantic, Thesis, Master of Science, University of Washington, Seattle. 178 p. (MS)

____________, Yield per recruit analysis for squid, *Loligo pealei* and *Illex illecebrosus*, from the Northwest Atlantic. J.Shellfish Res., 1(2) (in press)

Lange, A.M.T. and K.L. Johnson, Dorsal mantle length-total weight relationships of
1981 squids, *Loligo pealei* and *Illex illecebrosus*, from the Northwest Atlantic, off the coast of the United States. NOAA Tech.Rep.NMFS.(Spec.Sci.Rep.-Fish. Ser.), (745):17 p.

Lange, A.M.T. and M.P. Sissenwine, Biological considerations relevant to the management
1980 of squid *Loligo pealei* and *Illex illecebrosus* of the Northwest Atlantic. Mar.Fish.Rev., 42(7-8):23-38

Lyle, C.H., Historical statistics: the squid fishery. Curr.Fish.Statist.U.S.Bur.Commer.
1968 Fish., (4833). Issued also as Hist.Statist.U.S.Bur.Commer.Fish., (14):19 p.

Mercer, M.C., Contributions to the biology of the short-finned squid, *Illex illecebrosus*,
1965 (LeSueur) in the Newfoundland area. Manuscr.Rep.Ser.Fish.Res.Board Can. (Biol.), (834):36 p.

____________, Nominal catch of squid in Canadian Atlantic waters (Subareas 2-4) 1920-68.
1973 ICNAF Res. Doc. 73/73, Ser. No. 3025:10 p.

Mohn, R.K., Yield per recruit analysis of 4VWX squid by simulation. NAFO SCR No.
1981 81/VI/40, Ser. No. N322:15 p.

Paulik, G.J. and W.H. Bayliff, A generalized computer program for the Ricker model of
1967 equilibrium yield per recruitment. J.Fish.Res.Board Can., 24(2):249-59

Ricker, W.E., Handbook of computations for biological statistics of fish populations.
1958 Bull.Fish.Res.Board Can., (119):300 p.

____________, Computation and interpretation of biological statistics of fish populations.
1975 Bull.Fish.Mar.Serv.Can., (191):328 p.

Roper, C.F.E. and C.C. Lu, Rhynchoteuthoin larve of Ommastrephid squids of the western
1979 North Atlantic, with the first description of larvae and juveniles of *Illex illecebrosus*. Proc.Biol.Soc.Wash., 91(4):1053-73

Roper, C.F.E. and R.E. Young, Vertical distribution of pelagic cephalopods. Smithson.
1975 Contrib.Zool., (209)

Sissenwine, M.P. and E. Bowman, An analysis of some factors affecting the catchability
1978 of fish by bottom trawls. Res.Bull.ICNAF, (13):81-7

Sissenwine, M.P. and A.M. Tibbetts, Simulating the effect of fishing on squid, *Loligo*
1977 and *Illex* populations of the northeastern United States. Sel.Pap.ICNAF, (2): 71-84

Summers, W.C., Winter distribution of *Loligo pealei* determined by exploratory trawling.
1967 Biol.Bull.Mar.Biol.Lab.,Woods Hole, (133):489-501

Thompson, W.E. and F.H. Bell, Biological statistics of the Pacific Halibut. 2. Effect
1934 of the changes in intensity upon total yield and yield per unit of gear. Rep.Int.Fish.Pacif.Halibut Comm., (8):49 p.

Tibbetts, A.M., Squid fisheries *Loligo pealei* and *Illex illecebrosus* off the northeast
1975 United States ICNAF Subarea 5 and Statistical Area 6. ICNAF Res. Doc. No. 75/60, Ser. No. 3542:34 p.

Tomlinson, P.K., Program name--NORMSEP. Programmed by Victor Hasselblad. FAO Fish.
1971 Tech.Pap., (101):148 p.

STOCK ASSESSMENT OF CEPHALOPOD RESOURCES IN THE NORTHWESTERN PACIFIC

by

Masanao Osako and Mamoru Murata
Hokkaido Regional Fisheries Research Laboratory
Katsurakoi 116, Kushiro
Hokkaido, Japan

ABSTRACT

This report outlines the status of major Japanese fisheries for "Surume Ika" *(Todarodes pacificus)* and "Aka Ika" *(Ommastrephes bartrami)* and reviews the methods of recruitement forecast and stock assessment used for these two squid. Japanese domestic fisheries and studies on other cephalopods are briefly discussed.

In Japan many kinds of marine products are utilized, and a variety of methods of processing and use have developed. Many cephalopods are coastal in distribution and easily fished by simple gears such as squid jigs. Although cephalopod fisheries in the world have recently increased, Japanese catches still account for about 50 percent of the world total.

As mentioned above, there are many types of fisheries for cephalopods in Japan, but most, except for "Surume Ika" and "Aka Ika" jigging fisheries, are coastal, and land only small catches (about 20 000 t of cuttlefish and 50 000 to 60 000 t of octopus). In the "Surume Ika" fishery the greater part of catch is taken by jigging boats and from 5 to 500 GRT. Annual catch of "Surume Ika" was between 50 000 t and 200 000 t up until 1945 and sharply increased from 1945 through 1955. Three peak years of catch occurred during 1950 through 1970 in each of which annual catch was about 600 000 t. Since 1970 however, the catch has decreased to around 200 000 t. These three catch peaks correspond well to the expansion of fishing grounds of fisheries and new fishing gear. It now seems that all "Surume Ika" fishing grounds around Japan have been completely exploited since 1971.

In 1974 the "Aka Ika" fishery began in response to poor success of the "Surume Ika" fishery. This fishery now takes nearly the same catch as in the present "Surume Ika" fishery. Since 1978 a drift-gillnet fishery for squid has been introduced.

Cuttlefish is taken by bottom trawl in the East China Sea; octopus in the Seto Inland Sea and coastal areas of Hokkaido; "Kensaki Ika" *(Loligo edulis)*, "Yari Ika" *(Loligo bleekeri)*, "Sode Ika" *(Thysanotheuthis rhombus)* and "Hotaru Ika" *(Watasenia scintillans)*, etc. all in various local areas in Japan. Oceanic squid, "Tsume Ika" *(Onychoteuthis borealijaponica)*, "Tako Ika" *(Gonatopsis borealis)* and "Dosu Ika" *(Gonatus magister)*, etc. are fished incidentally.

Forecast and estimation of squid recruitment are made and announced officially twice a year in a cooperative meeting of national and prefectural institutes. Meetings are held before and in the middle of the fishing season for the Japan Sea ("Surume Ika") and the Pacific Ocean ("Surume Ika" and "Aka Ika") stocks. Data on size composition, larva, water temperature, catch statistics, CPUE, etc. are used for forecasting. No overall management of the Japanese squid fishery has been established to present however.

The relation between supply and demand of marine products is naturally balanced in Japan, but the high productivity of Japanese coastal waters is the reason why fisheries exploitation has proceeded well ahead of research, thus making fisheries management difficult.

Recently population dynamics has become a main theme of study on squid. Some preliminary work suggests that there is a relation between recruitment and fishing effort for "Surume Ika" and "Aka Ika" stocks around Japan, although there is much to be desired in the data base and methods used. With reference to "Surume Ika" and "Aka Ika" stocks, an analysis of the effect of the fishery on the stock and reproduction is an urgent priority.

RESUME

Ce rapport décrit la situation des principales pêcheries japonaises de "Surume Ika" *(Todarodes pacificus)* et "Aka Ika" *(Ommastrephes bartrami)*, et examine les méthodes de prévision des recrutements et d'évaluation des stocks utilisés pour ces deux espèces de céphalopodes. On examine aussi brièvement les pêches intérieures japonaises et des études sur d'autres céphalopodes.

On utilise au Japon une grande variété de produits de la mer et diverses méthodes de traitement et d'utilisation y ont été mises au point. Un grand nombre de céphalopodes vivent dans les eaux côtières et peuvent être pêchés au moyen de simples engins tels que la turlutte. La pêche aux céphalopodes a récemment pris de l'expansion dans le monde, mais les captures japonaises représentent encore environ 50 pour cent de la totalité des prises mondiales.

Ainsi qu'on l'a mentionné ci-dessus, il existe de nombreux types de pêches aux céphalopodes au Japon mais la plupart des bateaux qui utilisent la turlutte à l'exception de ceux qui exploitent le "Surume Ika" et le "Aka Ika", opèrent dans les eaux côtières et ne débarquent qu'un modeste volume de captures (environ 20 000 t de seiches et 50 000 à 60 000 t de poulpes). En ce qui concerne le "Surume Ika", une grande partie est capturée par des bateaux à turlutte de 5 à 500 TJB. Les captures annuelles de "Surume Ika" qui s'établissaient entre 50 000 et 200 000 t jusqu'en 1945 ont augmenté rapidement entre 1945 et 1955. Entre 1950 et 1970, on a enregistré trois années record au cours desquelles les captures annuelles s'établissaient à environ 600 000 t. Cependant, depuis 1970, les captures ont diminué pour tomber à environ 200 000 t. Ces trois années record de captures correspondent bien à l'expansion des fonds de pêche, à celle des pêcheries et à l'emploi de nouveaux engins de pêche. Il semble désormais que tous les fonds de pêche de "Surume Ika" aux alentours du Japon aient été complètement exploités depuis 1971.

En 1974, on a commencé à pêcher le "Aka Ika" parce que la pêche du "Surume Ika" donnait de mauvais résultats. Actuellement on capture presque la même quantité de "Aka Ika" et de "Surume Ika". Depuis 1978, on pratique la pêche aux céphalopodes à l'aide de filets maillants dérivants.

Les seiches sont capturées avec des chaluts de fond dans la mer de Chine orientale; les poulpes dans la mer intérieure de Seto et dans les eaux côtières de Hokkaido; le "Kensaki Ika" *(Loligo edulis)*, le "Yari Ika" *(Loligo bleekeri)*, le "Sode Ika" *(Thysanoteuthis rhombus)* et le "Hotaru Ika" *(Watasenia scintillans)* etc., sont tous capturés dans diverses mers japonaises. Les céphalopodes oceaniques "Tsume Ika" (*Onychoteuthis borealijaponica*), "Tako Ika" (*Gonatopsis borealis*) et "Dosu Ika" (*Gonatus magister*), etc., ne sont pêchés qu'accidentellement.

Les prévisions et estimations du recrutement des céphalopodes sont faites et annoncées officiellement deux fois par an au cours d'une réunion conjointe des institutions nationales et préfectorales. Des réunions relatives aux stocks qui se trouvent dans la mer du Japon ("Surume Ika") et à ceux qui se trouvent dans l'océan Pacifique ("Surume Ika" et "Aka Ika") ont lieu avant et au milieu de la saison des pêches. Des prévisions sont établies d'après les données concernant la composition par tailles, les larves, la température de l'eau, les statistiques des captures, les CPUE, etc. Cependant, il n'existe actuellement aucune politique globale de gestion de la pêche japonaise des céphalopodes.

Le rapport entre l'offre et la demande des produits de la mer est naturellement équilibré au Japon, mais la haute productivité des eaux côtières japonaises explique pourquoi l'exploitation des pêcheries a progressé beaucoup plus rapidement que la recherche, ce qui fait obstacle à la bonne gestion des pêches.

Récemment, la dynamique de population est devenu le thème principal de l'étude sur les céphalopodes. Certains travaux préliminaires laissent à penser qu'il existe un rapport entre le recrutement et l'effort de pêche en ce qui concerne les stocks de "Surume Ika" et d'"Aka Ika" aux alentours du Japon, même si la base de données et les méthodes utilisées laissent beaucoup à désirer. En ce qui concerne les stocks de "Surume Ika" et d'"Aka Ika", il est necessaire de procéder d'urgence à une analyse de l'incidence de la pêche sur le stock et la reproduction.

RESUMEN

El presente informe describe la situación de las principales pesquerías japonesas de "Surume Ika" *(Todarodes pacificus)* y "Aka Ika" *(Ommastrephes bartrami)* y examina los métodos de previsión del reclutamiento y estimación de poblaciones utilizados para estos dos tipos de calamares. Se resumen brevemente las pesquerías nacionales japonesas y los estudios nipónicos sobre otros cefalópodos.

En el Japón se emplean numerosos tipos de productos marinos y se han desarrollado diversos métodos de elaboración y utilización. Muchos cefalópodos son costeros por su distribución y se pescan con facilidad con artes sencillas, como las calamareras. Aunque recientemente han aumentado las pesquerías de cefalópodos en el mundo, las capturas del Japón representan aún aproximadamente el 50 por ciento del total mundial.

Como se ha mencionado más arriba, existen muchos tipos de pesquerías de cefalópodos en el Japón, pero la mayor parte, exceptuadas las pesquerías de "Surume Ika" y de "Aka Ika" con calamareras, son costeras y sólo desembarcan capturas pequeñas (approximadamente 20 000 t de jibia y de 50 000 a 60 000 t de pulpo). En la pesquería de "Surume Ika", la mayor parte de las capturas se efectúan mediante embarcaciones calamareras de 5 a 500 TRB. Las capturas anuales de "Surume Ika" totalizaron entre 50 000 y 200 000 t hasta 1945, para aumentar luego rápidamente desde 1945 hasta finales de 1955. Entre 1950 y 1970 se produjeron tres años récord de capturas, en cada uno de los cuales las capturas anuales totalizaron alrededor de 600 000 t. Sin embargo, desde 1970 las capturas han disminuido a un total aproximado de 200 000 t. Los tres récords de captura mencionados corresponden a la expansión de los caladeros y las pesquerías y a la introducción de nuevas artes de pesca. Actualmente parece ser que todos los caladeros de "Surume Ika" alrededor del Japón están ya plenamente explotados desde 1971.

Dado el poco éxito obtenido en la pesca de "Surume Ika", en 1974 comenzó la pesca de "Aka Ika" que hoy día proporciona aproximadamente las mismas capturas que la pesquería de "Surume Ika". Desde 1978 se ha introducido la pesca con redes de enmalle de deriva para el calamar.

Se capturan jibias con artes de arrastre de fondo en el mar de la China oriental, pulpos en el mar interior de Seto y en las zonas costeras de Hokkaido, y "Kensaki Ika" *(Loligo edulis)*, "Yari Ika" *(Loligo bleekeri)*, "Sode Ika" *(Thysanoteuthis rhombus)* "Hotaru Ika" *(Watasenia scintillans)*, etc. en diversas zonas locales del Japón. Accidentalmente se pescan también calamares oceánicos, "Tsume Ika" *(Onychoteuthis borealijaponica)*, "Tako Ika" *(Gonatopsis borealis)*, "Dosu Ika" *(Gonatus magister)*, etc.

Se hacen revisiones y estimaciones del reclutamiento de calamares, que se anuncian de manera oficial dos veces al año en una reunión conjunta de institutos nacionales y de las distintas prefecturas. Para las poblaciones del mar del Japón

("Surume Ika") y del Océano Pacífico ("Surume Ika" y "Aka Ika"), se celebran reuniones antes de la temporada de pesca y a mediados de la misma. Para hacer las previsiones se utilizan datos sobre composición por tallas, larvas, temperatura del agua, estadísticas de capturas, CPUE, etc. Sin embargo, hasta el momento no se ha establecido una disciplina global para la pesquería de calamar.

En el Japón, la relación entre la oferta y la demanda de productos marítimos se encuentra equilibrada de manera natural, pero la alta productividad de las aguas costeras japonesas ha hecho que las explotaciones pesqueras hayan avanzado muy por delante de las investigaciones dificultando así la ordenación de las pesquerías.

Recientemente, la dinámica de la población ha llegado a ser un tema fundamental de los estudios sobre el calamar. Algunos trabajos preliminares sugieren que, por lo que se refiere a las poblaciones de "Surume Ika" y "Aka Ika" que se encuentran alrededor del Japón, existe una relación entre el reclutamiento y el esfuerzo de pesca, aunque la base de datos y los métodos utilizados dejan mucho que desear. Es urgente hacer un análisis de los efectos de la pesca en la población y la reproducción de los calamares "Surume Ika" y "Aka Ika".

1. INTRODUCTION

Japan is not favoured with arable land, and domestic animals have been used as helpers for cultivation of land rather than as protein resources. This is why marine products, abundant and easier to obtain, have been preferably used in Japan as a food. Ancient shell mounds are found in the coastal areas in large numbers, and there is evidence that sea cucumbers and sea urchins were eaten in many places, indicating that Japanese people have long and strongly been associated with sea foods. It is then natural to guess that the use of marine products began with this easy access and that continued use established a favoured place for these commodities among Japanese foods. In the course of long history, the development of new methods of fishery, as well as the survival of those fish species chosen to meet the demand, must have contributed to the establishment of the contemporary Japanese fishery.

The history of the Japanese fishery for cephalopods is very long. The existence of cuttlefish shells in ancient shell piles proves that littoral cephalopods were used as an important protein resource even in ancient times.

At present cephalopods are relatively underutilized in the world, despite their widespread occurrence and local abundance. This is leading many countries to take a growing interest in them, with the realization that they are no less important than other protein resources. A report entitled "Stock Assessment of Cephalopod Resources Fished by Japan" (FAO, FIRS/T 173, 1977) described the situation of the Japanese fisheries in 1977 as part of a cooperative project of UNEP and FAO. No major changes have occurred in these fisheries since then, although as noted by Sato and Hatanaka (this publication). The establishment of Exclusive Economic Zones (EEZs) has promoted many countries to look closely at the problems of managing their coastal resources of cephalopods. Although as noted by the above authors, this has often adversely affected Japan's high-seas fisheries for cephalopods. Japan's long domestic experience with this type of fishery must be of great interest to these countries also.

In the present report, the author discusses firstly, the status of the "Surume Ika" (*Todarodes pacificus)* and "Aka Ika" *(Ommastrephes bartrami)* fishery, one of the main fisheries of Japan; then questions relating to the fisheries forecast and its relation to the migration of these squid to the fishing grounds are discussed, and lastly, the stock assessment of these species on the basis of the latest information. An outline of fisheries for other species of cephalopods will also be given later.

2. PRESENT STATUS OF CEPHALOPOD FISHERIES IN JAPAN

From an oceanographic point of view, the northwestern Pacific is defined as a region between the northwestern Pacific ridge stretching south of the Komandorskiye Islands and the ridge ranging from the Izu Islands to Tokobei Bay. Since this definition does not include all the areas exploited by the Japanese fishery in the region, the "Pacific Northwest" described as a statistical area in the FAO Yearbook of Fishery Statistics is also used in the present paper. Only the regional fishery by Japan is outlined here, because the author is not familiar with cephalopod fisheries conducted by other countries in this region.

Until recent years, the cephalopod catch around Japan accounted for 40 percent of the world catch; nearly 50 percent of the catch coming from the Japanese distant water fleet (Table 1). However, in recent years the Japanese share of the catch has gradually fallen below 50 percent of the world catch, partly because the catch of other countries has been increasing, and partly because the catch of "Surume Ika" *(Todarodes pacificus)*, the main cephalopod species in waters adjacent to Japan is decreasing (Table 2). Squid make up the largest proportion of all cephalopods caught around Japan. "Surume Ika" used to take first place among all the squid caught until 1974, when the fishery for "Aka Ika"*(Ommastrephes bartrami)*, another squid species, began (Table 3). Variations in the cephalopod catch in Japan depends greatly on the catch of these two squid. Catches of cuttlefish and octopus are not large, less than 20 000 and 60 000 t, respectively (Figure 1).

Many species of cephalopods are taken in different fisheries in Japan (Table 4). Of these, "Surume Ika" is caught in open waters, mostly by angling (Table 5). Other species of cephalopods are taken incidentally to other fish or in the coastal fisheries in many areas, by a variety of fishing gears (Tables 6, 7 and 8). Of these fisheries the octopus fishery is conducted with its own specific fishing gears and methods. However, landings are not distinguished by methods in the statistics (Table 8). The main forms of cephalopod fisheries are outlined below.

2.1 "Surume Ika" *(Todarodes pacificus)*

2.1.1 History of catch

Probably in ancient Japan squid and cuttlefish must have already been among the important species as now. However, it was not until from 1661 to 1741 that squid acquired an important position in the Japanese fishery when dried squid such as "Surume Ika", "Kensaki Ika" (*Loligo edulis*) and "Yari Ika" *(Loligo bleekeri)* became major trade goods, along with seaweeds, dried abalones and dried sea cucumbers. With the then current primitive fishing methods, littoral squid and cuttlefish must have been the main species fished, because their catch needed only such simple equipment as angling gears. With increasing demand, the fishing grounds spread offshore chiefly aiming at "Surume Ika".

The "Surume Ika" fishery became prosperous in 1864, when dried squid was exported from Hakodate Harbour to China under the Ch'ing Dynasty. The catch of "Surume Ika" amounted to between tens of thousands to 200 000 t until 1945; then it increased considerably between 1945 and 1955. For one thing, in the times of depression following the Second World War, the squid fishery was one of the few industries that could be expanded without much capital. For another, an increasing demand from Southwest Asia for the export of dried squid stimulated the catch of "Surume Ika". Later the catch varied a great deal from year to year until 1970, when the decline in landings started. In 1980, however, a tendency toward a gradual increase again became evident (Figure 2).

The majority of "Surume Ika" are fished by squid jigs, and the rest are caught together with other fish by bottom trawling and trapnets (Table 5).

Fishing areas before 1945 were chiefly the coasts of the Sanriku district on the Pacific side and the coasts of Hakodate in the Tsugaru Straits. In the former fishing grounds "Surume Ika" can be fished in large numbers even with trapnets. In the Japan Sea, this fishery has been conducted since early times. During the Meiji (1868-1911) and Taisho Eras (1912-25) the inshore waters in Toyama Bay, and around Sado, Oki and Goto Islands were known to be good fishing areas (Figure 3). In those days simple angling gear (Figure 4) was used, and the small fishing boats with a crew of one to three men were not equipped with motors. These primitive fisheries continued unimproved until 1945-46, with the catch ranging from tens of thousands to 200 000 t.

After the Second World War the need for food supply increased the demand for "Surume Ika" with the natural result of a sharp increase in catch. The post war years can be roughly divided into four periods in terms of the rise or fall in catch. A greater part of the catch was taken along the Pacific coasts of northern Japan. With the development of the offshore fishery in the Japan Sea beginning in 1967, and the remarkable decrease in the catch along the Pacific coast beginning in 1971, the main catch came from the Japan Sea (Figure 2). The annual catch taken in the Japan Sea until 1967 ranged between 50 000 and 100 000 t, and increased sharply thereafter. Thus, the catch of "Surume Ika" in Japan largely came from the Pacific coasts of northeastern Honshu and Hokkaido before 1970, and from the offshore fishing grounds in the Japan Sea after 1971. The change in the four periods is outlined as follows:

Period 1: 1947-56 (142 000-555 000 t; average 364 000 t)

In this period the Pacific region off northern Japan produced the largest share, especially in waters off Hokkaido (Table 9).

The fishery was conducted with fishing boats and angling gear on much the same scale as before 1947. After 1950 some improvements were made to the angling gears ("Tombo" in Japanese); and new angling gears with two lines, each with five jigs ("Suzuran-zuri" in Japanese), were introduced (Figures 4-9).

Around 1955, the "Suzuran-zuri" were improved so that they could be rolled round a drum by hand. Tohoku district became the second best fishing ground after Hokkaido, with many fishing boats (20 to 30 t) equipped with motors and a crew of around ten men each.

Period 2: 1957-64 (216 000-566 000 t; average 405 000 t)

From late in the previous period to early in this period, the whole Japanese catch decreased, while that from northeastern Honshu and eastern Hokkaido showed some increase (Table 9). More and more improvements were made to angling gears and fishing methods in the course of this period of decreasing catch. Squid were fished from greater depths than before, by introducing hand-operated drum angling jigs from fishing boats fixed with sea anchors. Later in this period, automatic jigging machines came into use, and the number of jigs operated by one angler increased to between 60 and 80. In addition, fishing boats became much more efficient. The effect of fishing lamps on "Surume Ika" catch has never been clearly proved, but increased lighting power of fishing lamps must certainly have brought a higher rate of capture. With these improvements, fishing efficiency clearly advanced further than in the previous period.

Period 3: 1965-71 (348 000-637 000 t; average 431 000 t)

Main catches in this period came from eastern Hokkaido. This is because this ground was suited to the large fishing boats which started to be built after 1969. The catch in southern Hokkaido has stayed between 40 000 and 90 000 t after its drastic decrease beginning in 1956 until this period. In northern Honshu, the catch has been continuously decreasing since 1964. Eastern Hokkaido recorded a peak catch of 130 000-330 000 t, but the catch has also been decreasing gradually after 1970.

By this time almost all fishing boats were equipped with automatic squid angling machines and more fishing effort was being exerted than ever before.

Later in this period the catch along the Pacific coasts of northern Honshu and Hokkaido began to show a drastic fall after the final big catch of 330 000 t in 1969. In the same year a law was enforced that every fishing boat larger than 100 t must obtain a licence from the Minister of Agriculture and Fisheries. At the same time, exploitation of offshore fishing grounds was promoted, with the result of an increased catch in the Japan Sea (Figure 2). The catch increased to 200 000 t in 1970 and to 190 000 t in 1971, largely owing to an improved navigational capability of the larger fishing boats, maintenance of freezing equipment, and discoveries of good fishing grounds offshore in the Japan Sea.

Period 4: 1972-79 (190 000-443 000 t; average 295 000 t)

In this period the catch along the Pacific coasts of northeastern Honshu and Hokkaido showed a marked decline. The average catch was 154 000 t from 1970 to 1972, 54 000 t from 1973 to 1975, and 6 000 t from 1976 to 1979. This drastic fall outweighed the remarkable increase in the catch offshore in the Japan Sea, resulting in a continued decline in the total domestic catch from 1970 onward.

2.1.2 Changes in fishing grounds

As mentioned above, fluctuations in the catch can conveniently be characterized by four periods according to the dominant fishing grounds in use (Figure 3). In the period from 1965 to 1971 highly dense distributions of "Surume Ika" were found in the Pacific coast off the South Kuril Islands in the Okhotsk Sea. This discovery, together with an increase in the size of fishing boats, led a large number of fishing boats moving exclusively to these new fishing grounds, with remarkable increases in the catch resulting. However, at the same time the exploitation of fishing grounds for "Surume Ika" along the Pacific coast came to an end.

After the recorded highest catch of 670 000 t in 1968, the catch off the Pacific coast slowly began to decrease, until it fell below 10 000 t in and after 1976. In the Japan Sea on the other hand, as the result of successful exploitation of offshore fishing grounds starting in 1967, the number of fishing boats increased year by year and at the same time the fishing season was stretched to half a year, from June to November. In 1971, the number of boats fishing offshore at the peak of the fishing season reached 2 000 partly owing to a poor catch in the Pacific. However, after the peak of 180 000 t in 1972, the catch from offshore waters began to fall, until it reached a steady state at a level of 160 000 t from 1973 to 1975, then dropped further in 1976. There are several good fishing grounds offshore in the Japan Sea, especially off the west coast of Sakhalin that have very dense concentrations of "Surume Ika". According to accounts from various sources of information, the annual catch from 1972 to 1974 probably amounted to between 40 000 and 70 000 t. About 300 to 500 fishing boats were observed to have engaged in intensive fishing operations there (Murata, *per. comm.*). However, after 1977 fishing activity was prohibited in these waters by the 200-mi territorial limit enforced by the Soviet Union.

Decrease in the catch of "Surume Ika" prompted exploration for new fishing grounds. These were discovered in the adjacent waters south of the Kuril Islands (including the Okhotsk Sea) in the Pacific, and in the waters adjacent to the Maritime Province of Siberia and off the west coasts of Sakhalin in the Japan Sea (Figure 3). Now the phase of expansion of areas of exploitation was complete. Nevertheless, increased fishing effort in these new fishing grounds did not increase the catch, but has instead led to a steady decrease in the Pacific catch since 1969, and from the Japan Sea since 1976. The national "Surume Ika" catch of 1980 is estimated to be about 270 000 t. If this estimate is right, we can hope that landings will soon once more be on the increase.

2.1.3 Changes in fishing effort

Increasing exploitation of "Surume Ika" caused a shift in fishing grounds from nearshore to offshore, bringing corresponding changes in the size of fishing boats (Table 10). Non-motorized boats decreased year by year till they accounted for only 0.6 percent of the total in 1979, compared with 100 percent in 1958. Boats of less than 20 t, especially small boats of 2-3 t, are now equipped with motors. In the meantime, fishing boats of 20-30 t are being replaced by larger boats. This tendency began in 1969 and was more and more evident from 1971 onward. Since 1974, the number of boats of this size have decreased remarkably. In other words, boats of less than 20-30 t are now being directed to inshore fishing operations, while larger boats are being used offshore. Because of this tendency, the catch per fishing day of both categories of vessel have naturally changed since the 1970s (Table 11 and Figure 5).

Boats smaller than 5 t comprise a larger proportion of the fleet than any other type (80 percent in 1979). This high percentage can be readily explained as follows: a sharp rise in the price of "Surume Ika" promoted coastal fishing of this species and boats of this type are best suited for operation in the newly exploited inshore fishing grounds. On the other hand, boats of 20-30 t, which used to operate a little further offshore than the coastal waters, were replaced by larger boats, mainly 30-100 t, because of the need for longer trips. Large boats operate over a wide area extending from coastal to offshore waters throughout the year. Still larger fishing boats of more than 100 t now operate extensively further out at sea; in many cases a great distance from Japan; e.g., in New Zealand and Australian waters.

2.2 "Aka Ika" *(Ommastrephes bartrami)*

2.2.1 Development of the fishery

Although the distribution of "Aka Ika" in the Pacific coast adjacent to Japan has long been known, the species was never the object of fishery, partly because the demand never existed, and partly because the distribution was far out at sea. However, a drastic decrease in "Surume Ika" in Pacific waters from 1970 onward meant that "Aka Ika" became the new object of a directed fishery as a substitute. With increasing demand for the alternative species for processed foods, "Aka Ika" soon replaced "Surume Ika" as the chief target of the fishery in the Pacific region. Jigging boats were already capable of making long trips offshore where these squid are found, and the catch steadily increased, starting with 17 000 t in 1974 (Table 3). The "Aka Ika" fishery, which began with jigging, has now adopted a new method using drift gillnets since the 1978 fishing season. The fishery prospered, because improvements were rapidly made in the processing technique and new fishing grounds were quickly exploited in order to make up for the sharp decrease in the "Surume Ika" catch (Figure 6). The increased exploitation of the fishing grounds for "Aka Ika" was also facilitated by the development of the drift gillnet method. A problem arose, however, with this method. Since it showed a remarkably high capture efficiency compared with jigging (Table 12), it led to excessive fishing pressure on squid resources in the limited fishing grounds. Because of this, the Fisheries Agency banned the drift gillnet method in waters north of latitude 20°N and west of longitude 170°E on and after 1 January 1979. In consequence, fishing boats using drift gillnets for the "Aka Ika" fishery were obliged to move out to waters east of latitude 170°E.

Not all fishermen were able to overcome these conditions imposed on the fishing operation in more distant waters, as inadequate prices received were insufficient to pay for the costly equipment needed. Only some boats with certain qualifications were allowed to continue operating as before. However, the catch taken by drift gillnets amounts to a greater part of the whole "Aka Ika" catch as shown in Table 3. Therefore, from August 1981 onwards, the Japanese Government decided to limit this fishery only to those who are approved by the Minister. Jigging boats now operating in Japanese waters try to fish "Surume Ika" with its higher commercial value in the years of good catch, or "Aka Ika", abundant yet commercially not very valuable, in the years of poor catch of "Surume Ika". In other words, fishermen choose the object of their effort, depending on the catch of "Surume Ika" expected for the coming year. Detailed statistics of the drift gillnet fishery are still unavailable except for data received directly from some boats.

2.2.2 Fishing grounds

"Aka Ika" fishing starts in July, reaches a peak in August and continues to October, with a sudden fall in activity from November onwards (Figure 7). Fishing grounds have gradually spread far out at sea since the "Aka Ika" fishery began (Figure 6). The seasonal change of fishing grounds reveals that the operating areas move progressively northward from July to October while spreading east and west and then extend southward, concentrating in westernly waters from November to February (Figure 8). The main fishing grounds in the peak season are latitude 40° to 46°N and longitude 143° to 165°E. Small boats (less than 29 t) operate chiefly on fishing grounds west of longitude 150°E, medium boats (30 to 99 t) west of longitude 160°E, and large boats (more than 100 t) between longitude 150° to 165°E. As mentioned before, fishing grounds for drift gillnet fishery have been limited to waters east of longitude 170°E since 1979 (Figure 6). It is likely that the fishing grounds, situated within waters longitude 170°E to longitude 160°E, shift with the seasons from 38° to 39°N and 170° to 175°E to 49°N and 160°W before again moving back to southeastern waters.

2.2.3 Fishing gears

The "Aka Ika" fishery is the same as the "Surume Ika" fishery in fishing gears and methods, except that the jigs are bigger in the former. Automatic jigging machines are used to some extent, but compared with the "Surume Ika" fishery, a greater part of the catch is taken by handlining. Therefore, the larger a boat is, the larger the size of its crew, and the greater the fishing power. Since fishing by drift gillnets is confined to distant fishing grounds requiring long trips, this method is adopted by boats larger than 60 t. Nets with stretched mesh size between 110 and 120 mm are chiefly used. A unit size of drift gillnet 8 m high and about 50 m long is called one "tan" (one box) in Japanese. In the evening 500 to 800 "tans" of drift gillnets are set at the surface and hauled the following morning.

2.3 Cuttlefish

The cuttlefish fishery is generally carried out in coastal waters south of Tokyo Bay facing the Pacific and in Toyama Bay facing the Japan Sea. Catches from these grounds are shown in Table 13, which is based on Japanese fish landings by statistical division (Figure 9).

The origin of the cuttlefish fishery probably dates back to ancient times, in view of the wide distribution of the species in coastal waters around the country. Most cuttlefish are taken incidentally in fisheries for other species by small boats (less than 5 t) using squid jigs, small coastal trawls (nets called "pacchi" in Japanese) and small trapnets. Large bottom trawls are used in the East China Sea. In most cases cuttlefish is taken incidentally in fisheries for other species (Table 6). Occasionally, cuttlefish are the object of sport fishing.

The cuttlefish taken by bottom trawling in the East China Sea consist of "Kou Ika" *(Sepia esculenta)*, "Shiriyake Ika" *(Sepiella japonica)* and others, with the first mentioned as the main species. Information is scarce concerning these species and the exact amount of catches unknown, being included in the whole catch of unspecified cephalopods.

The cuttlefish fishery is most active in the Inland Sea, followed by the central part of the Pacific coast. The species taken in these waters consist of "Kou Ika", "Shiriyake Ika","Kaminari Ika" *(Sepia lycidas)* and "Himekou Ika" *(Sepia kobiensis)*. The cuttlefish in the Inland Sea are predominantly distributed in inshore waters of the Kii and Bungo Channels during spring and summer, while they move into the open sea outside these two channels during autumn and winter (Figure 10). The fishing seasons of the species correspond to the breeding and immature periods. Catch reaches a peak in the breeding season (April to July), and decreases thereafter till November through January, when the fishery becomes active again.

Both "Kou Ika" and "Shiriyake Ika" are believed to have a lifespan of one year. The former grows from larvae, about 3 cm long soon after hatching, to 12 cm (female) and 13 cm (male) in dorsal mantle length by the end of December. Likewise, male larvae of "Shiriyake Ika" reach 15 cm in length one year after hatching. The lack of sufficient information still makes it difficult to estimate the stock size, but efforts are being made to follow the state of the stock in order to maintain it as the object of a coastal fishery commanding a high market price due to strong demand.

2.4 Octopus

The chief species taken by the *Octopus* fishery in waters adjacent to Japan are "Ma Dako" *(Octopus vulgaris)* and "Mizu Dako" *(Octopus dofleini)*. Minor species include "Ii Dako" *(Octopus membranaceus)*, "Tenaga Dako" *(Octopus minor)*, "Yanagi Dako" *(Octopus conispadiceus)* and "Ezokumo Dako" *(Octopus araneoides)*.

One of the chief species, "Ma Dako", is distributed in waters south of central Japan, while the other species, "Mizu Dako", is found in waters around northeast Japan. The octopus fishery has a long history. Especially in the Inland Sea, almost all octopus grounds are fully exploited, and care is now being taken to preserve eggs and larvae in order to sustain stock abundance. On the other hand, the octopus fishery in Hokkaido is relatively new and since the fishing operation started in 1955, it has replaced the herring fishery which used to be prosperous but has since declined all around Japan.

Octopus changes its behaviour on reaching the benthic stage. Subsequently they show cryptic behaviour hiding themselves in holes; each tending to keep to its own territory. They do not live in groups which makes it necessary to fish them one at a time. Fishing methods which take advantage of this behaviour have been extensively adopted. Since only a limited number of octopus can inhabit a certain area, a major increase in their stock size can hardly be expected. Table 8 shows that most of the octopus catch is taken by fisheries classified statistically as miscellaneous.

The octopus fishery is diverse in its methods (Figures 4-2); using octopus pots or boxes (boxes are preferred in Hokkaido, because "Mizu Dako" taken there is larger than "Ma Dako"), trolling (a way of catching octopus by trailing baits over the sea floor), octopus longlining, and octopus spearing (catching octopuses by spearing them in their holes).

The following is an outline of the "Ma Dako" fishery in the Inland Sea and the "Mizu Dako" fishery in Hokkaido.

2.4.1 The octopus fishery in the Inland Sea

Figure 11-A shows the fishing grounds of the octopus fishery in the Inland Sea. The catch is taken incidentally in fisheries for other species by using pots, jigs and small trawl nets on fishing grounds in areas of rather swift current. "Ma Dako" being a warm water species becomes irregular in its feeding activity in water below 12°C and is inactive in water of 7°C. The species migrates vertically on a seasonal basis between the cold and warm water periods. The spawning period is twice yearly; April and May in spring, September and October in autumn; spring and autumn spawning groups being distinguishable The latter group is far larger in number and its spawning period comes between the beginning and the middle of September. During the spawning period female octopus hardly feed and stay on the eggs all the time. The number of eggs depends on the size of the parent octopus: an octopus about 1.2 kg in weight lays some 150 000 eggs. These are laid mainly in hollows under shoreline reefs, in old octopus pots or in empty cans. This species grows fast. Breeding experiments reveal that they begin to swim and feed soon after hatching and in forty days or so they reach about 12 mm in total length and begin a benthic life. They weigh 1 kg in about 140 days and go successively through stages of sexual maturity, copulation, spawning and death. Their lifespan is believed to range from one year to one and one half years. Recently in the Inland Sea some 12 000-17 000 octopus pots were placed on gravel bottom in an attempt to shelter spawning adults for the preservation of the resources.

2.4.2 The octopus fishery in Hokkaido

As mentioned before, the octopus fishery in Hokkaido has a relatively short history. The fishery has been active with a constant annual catch of 20 000 t since 1955 (Table 14). Around Hokkaido "Mizu Dako", "Yanagi Dako" and "Ezokumo Dako" are found of which the first species is the one mainly fished. The fishery is conducted almost everywhere around Hokkaido and a majority of the catch is taken on the Japan Sea side (Figure 11B; Table 15). The fishing gears exclusively used are octopus boxes, bare longlines ("karatsurinawa" in Japanese), and trolling ("tarunagashi" in Japanese) (Figure 4-2). A minor part of the catch is taken incidentally by bottom trawls for other species.

(a) The reason that wooden boxes are used instead of pots is that large pots would be too heavy to be easily hauled with the catch inside. The fishing season comes twice a year, May to August, and December to February. The fishing grounds are located on flat sandy or mud bottoms in waters 40-60 m deep. Boxes vary locally in size but most of them are 40, 30 and 20 cm in length, width and depth, respectively. Opening of boxes vary in form, such as hexagons, rhombuses, rectangles and circles.

(b) Bare longline, which were originally used for catching rays in Chiba Prefecture, turned out be very effective in catching octopuses when introduced to Hokkaido for the purpose of fishing species of skate. Since then, this fishing gear has been exclusively used for catching octopus. These hooked gears are set in passways in depths of 70-150 m to take octopus making vertical migrations at the copulation period, which comes twice a year, April to July and November to February.

(c) Trolling the octopus fishery is a method in which floating casks with hooks fixed on cast-iron plates trailed below them are trailed over the bottom in areas of relatively swift currents. The casks are hauled together with the catch when the weight of octopus hooked submerges the casks.

"Mizu Dako", "Yanagi Dako", "Ezokumo Dako" habitats are segregated according to water depth. The first species occurs between low water mark and 180 m depth and are fished by octopus boxes, trolling and bare longlines. The second species are chiefly found in waters deeper than 100 m and are taken incidentally with other species of fish in shrimp baskets, shrimp beam trawls and bottom trawls. The third species occurs in waters deeper than 200 m, and are also incidentally taken in fisheries for other species. They have little commercial value because they weigh only 300 g each as adults.

"Mizu Dako" spawn in nests on rocky or sand beds less than 50-60 m deep from May to June. Hatching takes 6-7 months and in Hokkaido hatching activity reaches a peak between November and December. Hatched larvae are approximately 10 mm long and continue planktonic lives till they reach 10-50 mm long around March the following year. Then they live benthically and after exceeding 1 kg they are considered to be a fishable size. When they weigh more than 10 kg, they enter the spawning stage with the gonad fully matured.

"Mizu Dako" big enough for fishing migrate periodically; approaching the coast between October and November, forming groups from December to January, then move back offshore from February to March. Again, they approach the coast between April and May, form groups from June to July, then go back offshore from August to September, thus making vertical migrations twice a year. The species grows relatively fast. Some adults reach 3 m long and weigh 30 kg, but most of them weigh less than 10 kg. A tagging experiment showed that a released octopus of 1 kg can weigh 10 kg when recovered a year later. Although the maturation and growth of the species is still a matter of conjecture, they supposedly weigh 120-130 g a year after hatching, 1-2 kg two years later and reach maturity at 10 kg in three years.

With the development of mature gonads, octopus distributed offshore gradually approach the coast and begin copulatory activity in waters less than 100 m deep. The peak in copulation occurs between November and December. Later, males go back offshore and die after several months, while females go on to spawning grounds in shallower waters. From May to June females weigh 10-15 kg and spawn. The number of eggs depends on the size of the parent; varying from 30 000-60 000.

As eggs are brooded until they hatch out, their survival rate is probably high. This species is fished mainly in Hokkaido at the immature stage.

2.5 Other Species of Squid

Many other squid species are fished in coastal waters by angling using squid jigs, trapnets and bottom trawls (Table 7). "Yari Ika" *(Loligo bleekeri)*, "Budo Ika" *(Loligo edulis budo)* and "Kensaki Ika" *(Loligo edulis)* are rather extensively fished, while "Sode Ika" *(Thysanoteuthis rhombus)* and "Hotaru Ika" *(Watasenia scintillans)* are locally fished. In north Japan "Dosu Ika" *(Berryteuthis magister)* is caught in bottom trawls, "Tsume Ika" *(Onychoteuthis borealijaponica)* and "Tako Ika" *(Gonatopsis borealis)* by using squid jigs.

2.5.1 "Yari Ika" *(Loligo bleekeri)*

"Yari Ika" is fished by trapnets and bottom trawls everywhere around Japan. Lately, this species, which is a shallow water species and makes no large migrations, has been extensively studied concerning the possibility of culture to assist with the preservation of the resource. For example, artificial spawning beds have been built on the sea floor, but the effect of this is not known yet.

The following three are the main fishing grounds for "Yari Ika":

(a) Coastal waters facing the Japan Sea, from Niigata Prefecture to south Hokkaido. In this region the largest catch by various fishing gears is loaded on the Aomori coast, each gear being well matched to the distribution pattern and the local migratory behaviour of the species (Table 16). That is to say, that immature and benthic dwelling squid are fished by bottom trawl in the autumn, and in winter when mature males at the stage of copulation approach the coasts, they are fished using squid jigs. From winter to spring, when the spawning period brings females nearer to the coast, they are fished by bottom set-nets ("sokotate-ami" in Japanese) in depths of 50-70 m and by "bouke-ami" (nets to catch squid attracted by fishing lamps at night). In spring when some groups approach close to the shore, they are caught by trapnets.

(b) Coastal waters of northwest Kyushu, Tsushima and Yamaguchi Prefecture. In this region "Surume Ika" and "Yari Ika", together with various species of fish, used to be caught by angling, but now they are fished by bottom trawls, with a marked increase in the catch initially. A deleterious effect of this fishing method has recently appeared in the form of a decided decrease in the catch by angling, and naturally by bottom trawls as well.

(c) Coastal waters in the Tohoku district from Fukushima to Iwate Prefecture. Here fishing is conducted by bottom trawls alone, with a catch much smaller than that on the two above fishing grounds.

Judging from fishing methods corresponding to the seasonal distribution pattern of "Yari Ika" and its spawning behaviour as mentioned above, it seems that this species is divided into three groups at least. Though the extent of interchange among these groups is unknown, each group is supposed to be independent. Fishing operations on each ground become most active when the squid approach tidal areas for spawning. This fishing season varies slightly with the locality; that is, it ranges from winter to spring in the south and from spring to summer in the north. Although the spawning behaviour, which takes place in relatively shallow water, is well known, there is no detailed information on the bahaviour of the species in the immature stage in summer and autumn after hatching.

2.5.2 "Kensaki Ika" *(Loligo edulis)* and "Budo Ika" *(L. edulis budo)*

These two species are fished chiefly in southwest Japan. In the west Japan Sea and west Kyushu they are caught by angling, and on the Pacific coasts of Shikoku by angling, which is most common, small bottom trawls, purse seines and large trapnets (Table 17).

Around Tsushima Island, northwest of Kyushu, "Kensaki Ika" is fished by angling using squid jigs. The species is generally supposed to migrate northward from spring to summer, while through summer into autumn it moves southward. Also on the fishing grounds ranging from west Kyushu to the East China Sea, the annual catch is taken by bottom trawl, angling and trapnets, and varies from 16 000-21 000 t (1968-77)(Table 17). Populations caught by bottom trawl in the East China Sea are believed to be biologically different from those taken in west Kyushu.

The squid fishery in west Kyushu is conducted mainly by boats smaller than 20 t, especially by small boats of less than 5 t or to be more precise, less than 3 t. The fishing season usually reaches a peak twice a year; in spring to summer and from summer to autumn. Early in the first period, April and May, the main fishing grounds are in coastal waters 20-40 m deep, but early in June the fishing grounds shift to offshore waters. From July to August fishing grounds are in waters deeper than 60 m, and from September to November in waters deeper than 60-100 m and further out to sea. There is not enough information available yet on "Budo Ika" to make an accurate estimate of the stock size of this species.

2.5.3 "Sode Ika" *(Thysanoteuthis rhombus)*

"Sode Ika" is usually distributed in the major current, the Kuroshio, and in the Tsushima Warm Current off Japan. Previously the species was generally known in San-in district (the westernmost area of Honshu), because it was often taken by trapnets in fisheries for other species, found drifted onto the seashore or attracted by fishing lamps set for "Surume Ika". However, its commercial value was not then fully realized, and only a small amount of catch was locally taken.

In recent times a fishery for this species started in east San-in waters and it has since become a new directed fishery, with improvements made in its commercial utilization and fishing method. There is still a lack of information, however, on its behaviour and migration, the cause of quantitative variations and other questions.

As mentioned above, this fishery began in 1962 and it has gone through large annual variations in operation since then (Table 18). This species is fished mainly by squid jigs and trapnets. Small fishing boats of 5 t or so are used for the fishery. At the peak of the fishing season about 200 boats are engaged in the operation. Fishing in this region has been conducted in the daytime since 1967 (Figure 4-1), with the average catch of 6-9 squid/boat, at the peak of the fishing season. As the new fishing method enables a variety of fishing gears to be used at the same time, it was decided that one boat should not use more than thirty units of gear.

The fishing grounds cover a wide area at the peak of the fishing season, suggesting that the distribution of "Sode Ika" is relatively wide. One squid caught often leads to another being caught nearby and this proves that squid of this species make the migration in pairs.

From water temperatures the range in the Japan Sea and the maturity process of the species, it seems unlikely that spawning takes place in this area. Sometimes specimens are found dead in bottom trawls or drift to the shore in a moribund condition, and it seems likely that in December, when the fishing season comes to an end, some species of a warm-water type find it impossible to make southward migrations because of sudden drop in temperature.

"Sode Ika" begin their migration into the Japan Sea when water temperatures reach 19°C. From late May to June when the water temperature rises, they are believed to migrate into the Japan Sea from southern areas, with the northward movement of the Tsushima Warm Current. The vertical distribution of water temperature recorded through the fishing period during years of good catches and poor catches shows that in the years of good catches water temperature at 100 m depth exceeds 17°C, while in the years of poor catches it is below 17°C.

Variations in the stock abundance of this squid species migrating into the Japan Sea seem to derive mainly from changes in sea conditions rather than changes in stock size.

2.5.4 "Hotaru Ika" *(Watasenia scintillans)*

Toyama Bay in the Japan Sea has been the only fishing ground of this species since ancient times. From mid-February to early July these squid are fished by trapnets, and the peak of the fishing season ranges from early April to early May. The annual catch varies from 800 to 3 700 t. The processed squid, much to the Japanese taste, are highly valued, making one of the important industries in this district.

"Hotaru Ika" is supposed to live on the continental shelves at or below 200 m depth except during the fishing season. On sexual maturity, copulation occurs in deep water between winter and spring. Males die after copulation and females alone enter tidal areas in schools for spawning and are caught in trapnets.

The characteristics of the fishing grounds seem to be related to the topology of the sea floor in the offshore from these areas, i.e., marine canyons lead into the coast, and there are narrow continental shelves. When approaching shore, squid are approximately 60 mm in dorsal mantle length. They remain near surface at night, lay eggs and die soon afterward. Hatched larvae are at first distributed on the surface, but when they reach 2.5 mm long they are believed to be distributed mainly in waters below 20 m, and probably migrate to greater depths as they grow. The lifespan of this species is presumed to be one year, although the pattern of their behaviour between the onset of benthic life in deep water far offshore until the coastward migrations, is unknown.

Variations in the annual catch of "Hotaru Ika" from 1953 to 1978, though rather large, are random and do not show any sign of a downward tendency. Recent variations, though rather drastic, still show no decreasing trend. There is no evidence from this that the resources are overexploited at present.

2.5.5 "Dosu Ika" *(Berryteuthis magister)*, "Tsume Ika" *(Onychoteuthis borealijaponica)* and "Tako Ika" *(Gonatopsis borealis)*

With a recent decrease in the main species sought by the squid fishery, "Surume Ika", oceanic squid of the northern areas, which were previously not much in demand, have now become the object of attention and concern. Although its behaviour is not well known, "Dosu Ika" is a main species in bottom trawl fishery. Mature squid of this species are widely distributed in the Japan Sea and in waters of the Kuril Islands and the Aleutian Islands from 200 m to more than1 000 m deep. They tend to live in deeper waters in the southern part of the region and large catches are taken on slopes of the continental shelves from 200 to 500 m depth (Figure 12). North of the Kuril Islands, the peak of the fishing season ranges from July to October and in other months large catches are rare.

Catches of this squid, when taken by bottom trawling between spring and autumn, consist of mature females and males. Information available now indicates that they migrate toward the coast for the spawning period.

Since salmon, trout and especially silver salmon, often contain hatched larvae of "Dosu Ika" and immature individuals about 50 mm in dorsal mantle length in their stomachs, specimens of this species are believed to be distributed in relatively shallow water in the larval and juvenile stages and only enter the spawning stage following the onset of benthic life.

"Tsume Ika" is chiefly distributed off the Pacific coast of north Japan (Figure 13) and is taken incidentally by angling for "Surume Ika" and "Aka Ika" off the Pacific coast of east Hokkaido. The fishery for this species is, however, not very active, because it is not much in demand. This species, and other oceanic squid, such as "Aka Ika" became commercially exploited as a result of the decline in the fishery for "Surume Ika". Nevertheless, the commercial exploitation of this species has not increased much, and only a small amount of catch is landed, incidental to other species. One result of the drift net survey is that it is known that "Tsume Ika" is widely distributed far out to sea, east of Hokkaido and Sanriku from April to May, but is rather low in abundance. The catch taken incidentally in fisheries for other species increases to some extent between June and July. The species is distributed mainly north of 45°N and from 150°E to 180°E (Figure 13). These squid include individuals at different stages of growth. This difference in the stages of maturity suggests that their spawning season covers a long period from autumn to winter, and that some populations are hatched at different periods, as is the case for "Surume Ika" and "Aka Ika".

In autumn the males are less abundant and females appear more frequently in catches. Catches drop to zero by winter and hatched larvae are found in the water column from 80 to 200 m depth. Probably some biological change takes place in mature males and females at spawning.

"Tako Ika", as well as "Tsume Ika" appear towards April, and in May they are widely distributed east and west in the northwest Pacific, though they are not found in large numbers (Figure 13). From June to July they increase in number and are widely distributed in the Pacific from the south Kuril Islands to the southern tip of the Kamchatka Peninsula and also in waters 46°-47°N in the vicinity of 17.5°E.

Catches taken by angling are not large compared with other squid species, and the water temperature in the areas of distribution is lower than for "Surume Ika", "Aka Ika" and "Tsume Ika". "Tako Ika" consists of two populations: one smaller than 19 cm in dorsal mantle length and the other larger. Relations of growth and maturity between these two populations are still unknown, and there are also some differences in this distribution pattern. The behaviour of this species has not been well studied and many details of its biology are not clear. Since these squid are now taken incidentally in fisheries for other species, they are not considered to be an important commercial species.

3. FISHERIES FORECASTS TODAY

Scientists from Regional Fisheries Research Laboratories and Prefectural Fisheries Experimental Stations hold annual meetings in order to make fisheries forecasts for the main species of fish and cephalopods taken around Japan. Only the two main species of squid, "Surume Ika" and "Aka Ika" *(Todarodes pacificus* and *Ommastrephes bartrami)*, are the subjects of such a forecast. Forecasts for "Surume Ika" cover all fishing grounds in the Japan Sea and the Pacific, and forecasts for "Aka Ika" cover squid jigging grounds in the Pacific.

Such meetings for the purpose of making fisheries forecasts are held both before the fishing season in summer (June to September) and in autumn (October to December). Further meetings are held after the fishing season to carry out comprehensive examinations of the fishing conditions prevailing in the period and any changes in the stock. The Regional Fisheries Research Laboratories and Prefectural Fisheries Experimental Stations are responsible for assembling data for these meetings.

The 200-mi territorial limit was established around Japan in 1977, and since then every fishing boat has had to report on its daily operations. This has enabled the authorities to collect information on the squid catch for each fishing ground, and although this system has not worked perfectly, better information as a basis for stock size evaluations has now become available.

The "Aka Ika" fishery using drift gillnets developed during 1978 and was enforced by an approval system established by the Ministry of Agriculture, Forestry and Fisheries in August 1981. By legislation the catch statistics were also systematized at the same time.

Studies on the fishery resources of Japan have often been made only after extensive fishing, since the abundant resources have not needed management. However, the development of fishing techniques has brought the exploitation of important fish species to such a level that further increase in fishing effort does not always result in an increase in catch, and recently there has been a growing interest in understanding fluctuations in status of stocks of certain squid species.

3.1 "Surume Ika" *(Todarodes pacificus)*

Fishing forecasts for this species are designed to predict its abundance in the Japan Sea and the Pacific, and also in each of local fishing grounds based on a comprehensive evaluation of: (a) its life cycle as far as it has been established; (b)the occurrence of young and immature squid off the various coasts before the fishing season; (c) the results of surveys made by research vessels previous to each fishing season in summer and autumn; (d) oceanographic data, and (e) changes in stock status estimated from an analysis of the catch statistics and from data on larval distribution.

3.1.1 Spawning and migration

The location of spawning grounds for "Surume Ika" can be surmised from those areas where mature squid are fished, and where hatched larvae are found in large numbers (Figure 14). Judging from periodic differences in their growth and maturity, the resources of "Surume Ika" are generally assumed to be made up of three populations with different spawning times: a winter population, a summer population and an autumn population (Table 19).

The winter population is widely distributed around Japan, and forms a majority of the catch from the Pacific. The summer population appears along many coasts around Japan, but are not fished unless mature. They are found in coastal waters along the Japan Sea, and are considerably less abundant than the other two populations. The autumn population is widely distributed in the Japan Sea and is a major object of fishing. This population is also found in small numbers in the Pacific, and is fished in waters adjacent to Tohoku and Tokai districts.

The winter population has its main spawning grounds in the East China Sea, and its spawning season ranges from January to March. Larvae of this population are distributed from the south coast facing the East China Sea, to the southwestern coasts of Kyushu and Shikoku (Figure 15). A majority of these larvae migrate northward with the Kuroshio current in the Pacific, and some to the Japan Sea with the Tsushima Warm Current. They grow from juveniles into adolescents in the course of this migration and are fished by angling, trapnets and bottom trawls off various coasts. From catch information and from tagging they have been theorized to migrate both southward and northward (Figure 14).

The summer population has spawning grounds from the coast of Honshu to the East China Sea, and its main spawning grounds are considered to be located along the San-in coast in the Japan Sea. Larvae hatched from May to July probably grow and mature on the northward migration, but details of their growth are not known.

Spawning grounds for the autumn population are chiefly in the Japan Sea from the San-in district to the north and west of Kyushu, and on the Pacific side scattered in waters adjacent to Izu. Larvae of these populations are found inwaters a little to the north of the spawning grounds (Figure 16). The distribution pattern during the period when they grow into the immature stage is very little known. The immature squid migrate northward mainly to the vicinity of the polar front of the Japan Sea, then further north into the cold waters of the Liman Current system, and in summer to the west coast of Sakhalin, and towards the end of August when they reach the copulating stage, they start migrating southward.

Results of tagging experiments show that their migration usually is northward in spring and summer, and then southward in autumn, but that the movement is not always uniform (Figure 17). This somewhat complicated migration pattern is considered to be caused by intrinsic and extrinsic factors, such as the mixture of population at different stages of growth and changes in ocean conditions.

3.1.2 Fishery forecasts for the Pacific fishing grounds

From the above data of the life cycle of squid, the following types of information are used for fishery forecasts in the main fishing grounds in Tohoku and Hokkaido:

(a) Squid landings from the winter fishery in the spawning period around the Tsushima and Goto Islands are considered a guideline.

(b) The abundance of "Surume Ika" larvae is estimated from the numbers of larvae taken in the inshore small mesh trawl ("Pacchi-ami" in Japanese) fishery for sardine larvae along the Pacific coast of Shikoku in winter, and also from abundance surveys of squid larvae in the Kuroshio Current. Later the progress of the fishery on various fishing grounds from spring to early summer is followed.

Areas to the south of Shikoku and the west of Kii Peninsula become fishing grounds towards May and these then expand to the east of Kii Peninsula, and to Izu Peninsula and Boso Peninsula. Populations fished on these grounds are assumed to be identical to those populations which move into coastal waters from the winter population making its northward migration, and a majority of these are likely to stay in the same waters till they grow to commercial size.

Apart from this population, the autumn population, which becomes mature in September, is distributed in the coastal waters around the Izu and Boso Peninsulas and is fished simultaneously with the winter population. Along the coastline of the Tohoku district, trapnet fishing starts in May and angling in June. In June, before fishing starts on the main fishing grounds, abundance surveys are carried out in the form of a grid survey by research vessels mainly off the Tohoku coast (Figure 18).

Tohoku and Hokkaido have other populations migrating from the Japan Sea by way of the Tsugaru Straits, as well as those migrating northward in the Pacific. Accordingly fishing conditions along individual coasts in the Tsugaru Straits are also considered. Combined, this information forecasts the stock size migrating into the northern waters off Tohoku and Hokkaido, and from relationships established between fishing and ocean conditions (Figure 19) it also predicts the fishing conditions for each fishing ground in the summer. These forecasts are not made with numerical values but with fishing levels, and are of relatively high accuracy.

From late August to early September, when the summer fishery is complete and "Surume Ika" has not begun its southward migration yet, research vessels make surveys of the abundance of "Surume Ika" in northern waters in preparation for the autumn fishery. At this time fishing is taking place on various fishing grounds, and stock size surveys are also in progress. Comprehensive use is made of the data gained from these surveys in order to review the abundance (Figure 20). Fishing forecasts for autumn are made on the basis of these results, with higher accuracy than for the summer fishery.

3.1.3 Forecasts for fishing grounds in the Japan Sea

Depending on fishing ground and period the "Surume Ika" fishery in the Japan Sea exploits different populations. Table 20 shows a summary of these populations.

The autumn population is the main object of fishing in the Japan Sea, and larvae distribution surveys have been made since 1972 in order to forecast stock size. Results of these surveys are used to estimate the stock size for the year of the survey and the following year.

In early June, ten research vessels conduct surveys throughout the Japan Sea, excluding the coast of the USSR Maritime Provinces. The purpose of these surveys is to determine the distribution pattern of "Surume Ika" and the ocean conditions. Ocean conditions have a strong influence on fishing grounds, since offshore populations (autumn populations) migrate northward along the boundary between the cold water currents and the waters of the Tsushima Warm Current. When the cold water currents approach Japan, the result is good fishing in some places, but occasionally it prevents squid populations from migrating northward. These year to year changes in migration behaviour are considerable. Research vessels conduct surveys with squid jiggers. The number of squid caught per jigger per hour is expressed as CPUE (catch per unit effort) (Figure 21). Distribution densities are determined from CPUE and a stock size index and density index are worked out (Table 21).

The patterns of appearance, distribution range and density index for squid larvae (Table 22) are calculated from the findings of larvae distribution surveys made in autumn (October to December) of the previous year and these are compared with the results of past surveys. However, the stock size is not yet expressed in numerical terms and the stock is only estimated in relative values.

For the Japan Sea, a comprehensive evaluation is made of fishing conditions in much the same way as for the Pacific, from changes in catch, changes in catch per medium-sized fishing boat per day, fishing conditions in different places, as well as from the above-mentioned survey results. It still happens, however, that the numerical values estimated from larva surveys do not correspond to the stock size derived from information available after the start of fishing. These differences are carefully reviewed for the various fishing grounds, and arise from the fishing conditions, from, for example, delayed growth, and from fluctuations in the rate of fishing of the fleet: the latter chiefly for economic reasons. In the Japan Sea, the three populations, winter, summer and autumn are all fished and they are mixed in some places. This mixing, as well as other unsolved problems, causes difficulties in making accurate fishing forecasts.

3.2 "Aka Ika" *(Ommastrephes bartrami)*

The fishing grounds for "Aka Ika" stretch far and wide in the open sea and the fishing period is later than for "Surume Ika". The late fishing period makes it difficult to obtain sufficient information before July, and forecasts in September are regarded as important. Forecasts for "Aka Ika" are made chiefly from its abundance on the basis of the following information:

(a) hypotheses on the population structure and behaviour from biological data;

(b) developments in stock size estimated from a thorough analysis of the catch;

(c) biological data obtained in the past and from fishery conditions, as well as results of squid distribution surveys by research vessels; and

(d) information received from fishing operations up until the forecast period.

3.2.1 Hypotheses related to structure of populations and their behaviour

"Aka Ika" are found throughout the north Pacific, but not in the East China Sea, the Japan Sea, the Okhotsk Sea and the Bering Sea, and they tend to swarm around the Subarctic Boundary in the waters on the north side from summer to autumn (Figure 22). This distribution is not continuous from east to west. The chart of density distribution shows that "Aka Ika" mainly occurs in the waters west of 156°E and east of 170°E, with a lower density in between (Figure 23). From the length of the dorsal mantle, "Aka Ika" fished by angling in August and September, can be divided according to their distribution: (a) those fished west of 160°E (b) 180° to 140°W, (c) 140° to 130°W (Figure 24). Also, drift gillnet catch data show that squid with 35-45 cm dorsal mantle length are found in region (b), where large squids are distributed to the north and smaller ones to the south.

Information gained from tagging (Figure 25) and periodic distribution patterns (Figures 8, 22), show the migration pattern of "Aka Ika" in waters west of 170°E as follows (Figure 26):

"Aka Ika" migrating into this area hatched in the Kuroshio counter-current area south of 35°N and west of 155°E during winter and spring. Probably these larvae stay in the area they hatched in till spring, but little is known of their behaviour. From May to August immature squid migrate northward or northeastward through the transition area of the Kuroshio and the Oyashio Current from 35° to 40°N, generally in longitudes 144°-145°E, 148°-150°E and 154°-155°E; the migration seeming to be related to the flow of warm waters from the Kuroshio. These northward migrating squid behave in the following manner: faster growing ones distributed further out at sea begin their northward migration earlier. From August to October immature and mature squid are distributed mainly in surface waters of 10°-20°C in the region of the Oyashio Current from 40° to 46°N or along the front of the current, and they appear to stay here longer than in any of the previous periods of development. From October and November onwards "Aka Ika" approaching peak maturity appear to begin migrating southwards with the increasing spread of cold waters. The southward migration route seems to be related to the southeastward flow of cold water (less than 10°C surface water temperature), but details are not yet known. These squid begin migrating southwards as they mature. Male "Aka Ika" mature earlier than females and their southward migration starts earlier. Later, females lay eggs in these waters; and the spawning period probably continues from winter to spring. The areas considered as their spawning grounds appear related to submarine features, such as shallow reefs, the vicinity of islands, sea mounts, ocean ridges, and ocean basins. At the same time, the spawning seems to take place at the surface and at medium depths. Information on the spawning grounds is, however, largely a matter of conjecture.

From the following seasonal changes in the dorsal mantle length, the lifespan of "Aka Ika" is considered to be about one year. As information has become available, it has been found that two different populations, one with an extremely large and one with an extremely small, dorsal mantle, appear at the same time. It remains doubtful whether this difference in length is caused by differences in spawning periods.

3.2.2 Changes in stock size

Indications of changes in stock size are obtained from a comprehensive evaluation of fluctuations in catch as classified by fishing ground, fishing period and type of fishing boats, fluctuations in CPUE and also biological changes (e.g., changes in dorsal mantle length).

On the basis of available information, fishing forecasts are made for populations distributed in the area west of 170°E which are considered different from the populations further east. In the waters west of 170°E, the catch is taken by angling, using squid jigs. The following are details of this population, particularly related to changes in the stock size up until 1979. As mentioned previously, the catch in the area showed a rapid increase until 1978. In 1979, however, it decreased drastically to about half of the year before (Table 3).

According to catch per unit effort figures (CPUE) which are used as an index of the abundance for a fishing ground, the catching reached a peak in 1977 and has been falling ever since (Table 23). The fishing grounds were fully exploited around 1978 and the CPUE for 1979 was a little lower than for 1978 (Tables 23 and 24). This trend was corroborated by other data, such as catch classified by sea areas or classified by type of fishing boats (Table 25). A comparison of good fishing grounds (number of 1° x 1° rectangles with over 1.0 or over 2.0 t CPUE) shows that, compared with the previous year, the values in the period August-October in 1979 were 30-40 percent lower in rectangles with CPUE over 1.0 t and 40-70 percent in rectangles with CPUE over 2.0 t (Table 26). However, the annual changes of CPUE do not correspond to catch in number per unit effort. In 1979 large-sized boats showed an increase in catch in number, through medium-sized and small-sized boats showed a decrease compared with the previous year (Tables 23 and 24). This seems to suggest a trend for "Aka Ika" to become smaller, though there is a problem to be solved in conversion from weight to numbers (Table 27). The dorsal mantle length of "Aka Ika" was the largest in 1976 and since then it has become smaller year by year (Figure 27). That is, a comparison by sea areas shows that in sea areas west of 160°E, where medium-sized and small-sized fishing boats chiefly operate, the dorsal mantle length in 1979 was about the same as in 1978, while in offshore waters, where large-sized boats chiefly operate the mantle length, tends to be smaller (Table 27 and Figure 28).

As seen above, the wieght of catch clearly shows an annual decrease in CPUE, but the number caught is increasing in some sea areas. This evidence suggests that the number of relatively small squid is increasing with a corresponding decrease in the number of large squid. Accordingly, the migratory stock size is supposed to have decreased from 1978 onward.

3.2.3 Survey of distribution of migratory populations

The numbers of squid caught per jigger per hour, estimated from results of grid surveys in June and from August to September, is considered to be a relative index showing the size of migratory populations before and after entering the fishing grounds.

Surveys of "Aka ika" Distribution Surveys in June show that squid are distributed in waters of more than 15°C surface water temperature in the south part of the sea area surveyed. Since these are considered to be part of the northward migratory populations, it is very difficult to estimate the total size of the migrating population (Figure 29). Surveys made in August and September reveal that "Aka Ika" are rare in coastal waters of less than 15°C but that there are many throughout the sea area under investigation (Figure 30). Surveys made in the same period in 1978 and 1979 correspond to the analysed results of the above fishery data in that the distribution in 1978 is somewhat wider than in 1979, and squid were found a little further to the north.

3.2.4 Fishing information

Since a knowledge of fishing conditions prior to early September is very effective in forecasting the year's catch, information concerning landings and CPUE of fishing boats from various locations is reviewed at fishing forecast meetings.

After due consideration of these data, fishing forecasts for the year are made public (catch, CPUE, fishing grounds, etc.). However, both fishing and research on "Aka Ika" have a comparatively short history, and insufficient information exists to fully explain charges in stock size, making forecasts less accurate than for "Surume Ika". Further, "Aka Ika" is not in such strong demand and not as highly priced as "Surume Ika". Furthermore, the fishing grounds for "Aka Ika" are more distant, thus incurring increased fleet costs; thus, the fishing effort for "Aka Ika" depends on whether the catch of "Surume Ika" is good or not. This unpredictability stands in the way of reliable fishing forecasts for "Aka Ika".

4. CEPHALOPOD RESOURCES IN WATERS AROUND JAPAN

Since Japan has a long shoreline and is surrounded by oceanic areas high in marine productivity, a large number of marine products have been utilized from ancient times. These abundant marine products have been supplied by the highly productive fishery resources in the waters around Japan.

With undeveloped fishing techniques it was possible to provide a good supply of marine products following the growth in demand, without considering the effects of fishing. Under such circumstances, exploitation always went ahead of management of fishery resources, so rich is the natural productivity of Japanese waters. In recent times however, these resources which have been to date plentiful, have been considerably influenced by exploitation by highly developed fishery techniques, as well as a decrease in productivity caused by pollution of some of the spawning grounds. As a result, some species have shown no increase in catch despite an increase in fishing effort.

In the meantime, 200-mi territorial limits have been established by many countries, and in Japan efficient ways of managing fishing resources have come under discussion in an attempt to promote an efficient use of all fishery resources in coastal waters. Efficient methods, however, have not yet been worked out, and this is also the situation for the management of cephalopod fisheries. In the following sections, stock assessments of cephalopod resources fished by Japan will be discussed as an aspect of fishery management.

4.1 "Surume Ika" *(Todarodes pacificus)*

Former research on "Surume Ika" resources rarely included any consideration of the role of population dynamics in the direct management of the resource. In Japan, changes in the stock size have often been discussed, and random fluctuations in catch, excessive catch and natural factors have usually been considered the cause of decreases in catch.

In the case of"Surume Ika" the annual fluctuations in catch of the winter population have been analysed by correlogram analysis (Kawasaki, 1973; Murata and Araya, 1970). This analysis shows that fluctuations in stock size of the winter population for the period 1910-76 reached a high point corresponding to cycles of 27-28 years, and that a relatively high peak is also seen with a 9-year periodicity (Figure 1). The catch fluctuations show that there is a difference between years before and after 1947, and those fluctuations in catch from 1947 to 1976 were analysed. As a result, the high point shows up on a 16-18 year cycle and secondary high points occur on a 9-year cycle. If the catch of "Surume Ima" is regarded as an index of fluctuations in stock size, it follows that the resource fluctuated in cycles of 27-28 years, 16-18 years and 9 years.

The fishing rate for "Surume Ika" was calculated from the results of tagging of the winter population (Table 28), and the possible effects of fishing on the resources were carefully examined (Murata and Araya, 1970). An analysis has been made on the basis of tagging experiments in the Japan Sea (Machinaka *et al.*, 1980). With the population dynamics parameters defined (Table 29), a total mortality coefficient set at 0.433, and mortality rate by tagging and recovery ratios by releasing stations varied arbitrarily, values for the fishing mortality coefficient and natural mortality coefficient were obtained (Table 30). The results of tagging experiments contain an element of uncertainty due to death caused by tagging and in the recovery ratios, so that the validity of the values obtained may be low.

An attempt has been made to work out annual fishing rates and stock sizes after a fishing intensity has been estimated from various fishing data (Araya, 1974). Here the fishing rate showed its largest value (0.5) in 1970, while the stock size was largest (1 089 x 10^3 t) in 1968, with a sudden decrease thereafter (Table 31). The reproduction curve is shown as a function of spawning stock size (= original stock size - catch) and stock size of recruits (= stock size the following year) (Figure 32). As shown, the correlation coefficient between the two sizes is low, but positive. The regression equation obtained gives a stock size of about 1.73 times the parent stock size. The appropriate fishing rate obtained from this is 0.42, and when compared with the fishing rates given in Table 33, it indicates overfishing from 1959 onward. Applying these values to the Ricker's curve, and considering that recruitment success as a function of stock size is rarely linear (Figure 32) leaves some problems, because basic numerical values applied to the curve are hypothetically calculated; nonetheless, the recent trend toward overfishing can be seen.

As mentioned previously, "Surume Ika" is distributed around Japan in three populations, each with different periods of spawning and hatching. However, they seem to have a considerable ability to shift or transfer to other populations in the course of reproduction, because the spawning periods are continuous and breeding grounds and feeding grounds are geographically close, and the lifespan of these species is one year. An attempt has been made to analyse changes in the stock size on the assumption that "Surume Ika" around Japan can, on the large scale, be regarded as one population (Doi and Kawakami, 1979).

First, the growth rate of each population at a different hatching period in the Japan Sea was theoretically determined from monthly determinations of the average dorsal mantle length and the average weight. Based on these values the rates of anabolism and catabolism for each population was estimated and thus the daily growth rate for each population could be calculated. According to the life cycle of "Surume Ika", the number of eggs, survival rates and monthly average survival rates from the young stage onward were determined, and the squid biomass was analysed by means of an assumed theoretical formula (Table 32 and Figure 33). From this result the effects of fishery on the resource was estimated for winter populations in the Japan Sea (Figure 33 and Table 33). These calculated results are compared with the stock size estimated from changes in the catch. Next, the catch taken in January and February around the Goto Islands in the coastal waters off northwest Kyushu, which are supposed to be near the spawning grounds, was compared with the catch from the winter population in the Japan Sea and the North Pacific from June to December in the previous year (Figure 34). From this, the stock size of the winter population in the Japan Sea was found. This analysis shows that the stock size of the winter population decreased to one seventh of its initial size in ten years (1965-75); the stock size decreasing by 18 percent a year; the decrease presumed to have been caused by excessive fishing. The fishing mortality coefficient per month (F) now is estimated to be 0.025, while the value of F permitting reproduction is 0.01. It follows that if fishing effort or catch has been made or taken within the range of about 40 percent of the previous catch, populations would not decrease as much as now.

"Surume Ika" distributed around Japan are evidently divided into three populations with different growth rates and maturity times. However, as Doi and Kawakami (1979) have suggested on the basis of available data, "Surume Ika" may be called a one-population species.

These three populations then need not be completely independent: rather, depending on the circumstances, they may be mutually related and not separate into independent populations. It then becomes possible to consider them as a single population. To substantiate this hypothesis, it may be insufficient to use data from only a single fishing ground, however the catch for January and February around the Tsushima straits, which is considered an index for the spawning population, shows a simple and clear relation to the total catch of "Surume Ika".

A factor in "Surume Ika's" behaviour is the seabed formations over the fishing grounds, steep valleys and ravines in the continental shelf are relatively good fishing grounds (Figure 35). "Surume Ika" populations seem to aim for such formations, and when moving to the continental shelf a population appears to stay for periods of time around such formations. It is however uncertain whether the reason for this residence is an upwelling at a submarine formation, its water temperature, the food available in the particular environment, or some other preference of "Surume Ika". The important northernmost fishing grounds where the winter population of "Surume Ika" migrates in large groups for feeding, are formed in waters adjacent to the south Kuril Islands (the Nemuro Strait and the area south of Iturup in the Pacific, and areas west of Sakhalin in the Japan Sea), and all have similar topographical features (Figure 35).

The populations which swarm into these fishing grounds from summer to autumn are considered to be either populations which pass the coasts around Japan, migrating northward as young, or populations which migrate north further at sea than the coastal fishing grounds. These migrating populations are somewhat different from those fished in large numbers in the past on the fishing grounds off Tahoku and South Hokkaido in the hatching period, and they probably use a different northward migration route and have different growth conditions, too. If these populations on the northern fishing grounds were the same as those migrating into fishing grounds off Tohoku and South Hokkaido, migration onto the fishing grounds would only depend on ocean conditions, and the same fluctuations in catch would occur on every fishing ground at almost the same time. However, changes in catch by fishing ground show that the decreases began in coastal waters and spread to offshore waters. With the development of new fishery techniques and with the northern fishing grounds fully exploited, the catch has become almost constant. This suggests that though populations migrating into the fishing grounds are related to one another, each population acquires a different behaviour pattern during the long spawning period in the extensive spawning areas. It may also be that as the stocks fluctuate, some changes occur at the chief spawning grounds or in the biological characteristics of the populations. About the northernmost last exploited fishing grounds it can only be said that in the Pacific the catch of "Surume Ika" has drastically decreased since 1968, and in the Japan Sea it has decreased since the good catches in the 1970s. However, winter populations in the Japan Sea have been gradually increasing since the fishery was prohibited on fishing grounds west of the Sakhalin Peninsula by the Soviet enforcement of the 200-mi territorial limit in 1977. In 1980 and 1981 the catch in January and February around the Tsushima Strait showed a remarkable increase. At present in the Pacific, medium-sized and large-sized fishing boats have shifted their fishing effort to the "Aka Ika" fishery and no fishing for "Surume Ika" has been recently undertaken in waters adjacent to the South Kuril Islands. Due to this, the "Surume Ika" catch along the Pacific coast is beginning to increase.

From the above-mentioned research results and recent changes in fishing conditions, a reduction in fishing seems to have had a strong influence on "Surume Ika" reproduction.

Considering the survey results, a permissible catch for "Surume Ika" around Japan can be allowed to range up to 400 000-500 000 t, the maximum in the past, and the value of F(0.1)calculated by Doi and Kawakami (1979) may serve as a standard.

4.2 "Aka Ika" *(Ommastrephes bartrami)*

Stock size and permitted catch for "Aka Ika", distributed in waters west of 170°E, are calculated on the assumption that they all belong to one population with a lifespan of about one year. The fishing rate for "Aka Ika" in this marine area was probably high from 1977 to 1979, judging from the seasonal changes in CPUE in 1979 and 1980 (Figure 36), the frequency of squid with regenerated arms (cut off by jigging)(Murata, Ishii and Osako, 1981), the range of the fishing grounds, and the change in number of operating days (Table 23 and Figure 6).

On the other hand, the decrease in dorsal mantle length observed in "Aka Ika" fished by jigging (Figures 27, 28) continued until 1979. Information available so far interprets this phenomenon as follows: there are two or three populations with different schedules of growth. The large-sized population, hatching early in the long spawning period migrates early onto the fishing grounds and is fished longer than the small-sized population. As a result, the small-sized population, which is a little later in hatching and migrating, is gradually increasing. From this interpretation, the fishery for "Aka Ika" until 1978 was probably too intense for the optimal reproduction of the resource.

"Aka Ika" are considered to eat more fish and grow faster than "Surume Ika". They feed on small-sized fish such as myctophids among others, and the dorsal mantle length reaches from 35 cm (males) to 40 cm (females) and the weight reaches from 1.3 kg (males) to 2 kg (females) in a year. Their adaptability to ocean waters, taking larger food and reaching a greater size as adults, place them in an ecologically higher position than "Surume Ika". Accordingly, the stock size in number is assumed to be relatively lower than "Surume Ika".

All considered, a reason for the decrease in the "Aka Ika" catch, seems to be overfishing caused by an increase in fishing effort to a level too high for the recovery capacity of the resource, starting as early as 1978. It is clear that the 120 000-150 000 t catch in 1977 and 1978 was too high for the reproductive capability of "Aka Ika" in waters west of 170°E. The catch should not exceed 80 000-100 000 t; a little larger than the catch in 1976.

4.3 Other Species of Cephalopod

Although there is not sufficient information to analyse the stock size of cuttlefish, the catch of this species seems to suggest that there is room for further exploitation of this resource. However, the "Shiriyake Ika" *(Sepiella japonica)* fishery in the Kii Channel has shown a decrease in catch and the reproductive capacity of the species is considered to be low.

For other species, such as "Kensaki", "Budo" and "Yari Ika" *(Loligo edulis, Loligo edulis budo, Loligo bleekeri)*, some information about their biological behaviour and fishing has only recently become available, but it is still insufficient to estimate stock sizes. For other species of squid and cuttlefish, only partial information on their distribution is available, and their possible value as a fishery resource has only recently begun to be considered. The lack of information makes it impossible to estimate the total exploitable stock size.

The exploitation of octopuses in the Inland Sea is total and methods of preservation of the resource have been discussed. The present fishery is closely managed. Though there is not enough information to analyse the stock size of "Mizu Dako" *(Octopus dofleini)* and "Yanagi Dako" *(Octopus conispadiceus)* around Hokkaido, available biological information and the actual conditions of the fishery show that there has been no great change in the annual stock sizes. The number of eggs laid ranges from 30 000 to 60 000 and they are protected by parents till they hatch, when they become objects of a fishery at a weight of more than 1 kg, and they have a low natural mortality. The scheduling of the fishing period, since it precedes spawning, helps in protecting the eggs, and the hatched octopuses grow fast and keep to their own territory. Population densities depend on availability of suitable habitations, and are subject to natural regulation. Fishing large numbers is not possible, and these species are expected to maintain relatively stable levels. They are however in danger of exposure to marine pollution because their spawning grounds are found in coastal waters. Adequate care must be taken to prevent pollution in these areas. Fisheries for all octopus species in coastal waters require a common feature, namely a protection in the spawning period. Management must be based on further information of their behaviour so that they may be protected from pollution.

5. REFERENCES

Adachi, J., 1979 Studies on the stocks of the common squid, *Todarodes pacificus* Steenstrup. Clues on the Estimation and the Forecasting of the Stock Level of the Autumn Population in the Japan Sea. Bull.Jap.Soc.Fish.Oceanogr., (34) (in Japanese with English summary)

Akabane, M. and S. Kubota, 1972 Some considerations for the migration and the formation of fishery ground of common squid, *Todarodes pacificus* Steenstrup, in the northeastern sea area of Japan. Bull.Tohoku Reg.Fish.Res.Lab., (32) (in Japanese with English summary)

Araya, H., 1967 Resources of common squid, *Todarodes pacificus* Steenstrup, in the Japanese waters. Ser.Fish.Res.Jap.Soc.Fish.Resour.Conserv., (16) (in Japanese)

__________, 1969 Relationship between migration and fishing ground formation of squid, *Todarodes pacificus* Steenstrup, in the Japan Sea coast of northern Tohoku and southern Hokkaido districts in summer. Bull.Jap.Soc.Fish.Oceanogr., Spec.no. (in Japanese with English summary)

__________, 1974 Some problems of the conservation for the jigging fishery resources of a common squid, *Todarodes pacificus* Steenstrup in Japan. Fish.Resour.Invest.Sci.Fish.Agency Jap.Gov., (16) (in Japanese with English summary)

Araya, H., 1976 Migration and fishing ground of winter subpopulation of the squid, *Todarodes pacificus* Steenstrup, in the northern waters of Japan. Bull. Hokkaido Reg.Fish.Res.Lab., (41)

Araya, H. and S. Kawasaki, 1962 On the locomotion of the squid, *Ommastrephes sloani pacificus* Steenstrup, in the Okhotsk Sea along the coast of Hokkaido during the autumn of 1961. Bull.Hokkaido Reg.Fish.Res.Lab., (25):11-9 (in Japanese with English summary)

Doi, T. and T. Kawakami, 1979 Biomass of Japanese common squid *Todarodes pacificus* Steenstrup and the management of its fishery. Bull.Tokai Reg.Fish.Res.Lab., (99) (in Japanese with English summary)

FAO, 1976 The Expert contributed papers submitted to Consultation of fishing for squid and other cephalopods. Supplement to the Report. Tokyo and Hakodate, Japan, 9-13 September 1975. FAO Fish.Rep., (170) Suppl. 1:150 p. Issued also in French and Spanish

Fugii, T., *et al.*, 1979 Oceanographical condition and distributions of fish species near the polar front. Bull.Jap.Soc.Fish.Oceanogr., (35) (in Japanese)

Fukuda, T. and Y. Yamashita, 1978 Studies on the octopus *(Paroctopus dofleini dofleini)* distributed in the Soya Straits and its adjacent water. J.Hokkaido Fish. Exp.Stn., 35(3) (in Japanese)

Hamabe, M., 1962 Embryological studies on the common squid, *Ommastrephes sloani pacificus* Steenstrup, in the southwestern waters of the Sea of Japan. Bull.Jap.Sea Reg.Fish.Res.Lab., (10) (in Japanese with English summary)

Hamabe, M. and T. Shimizu, 1966 Ecological studies on the common squid, *Todarodes pacificus* Steenstrup, mainly in the southwestern waters of the Japan Sea. Bull.Jap. Sea Reg.Fish.Res.Lab., (16):13-55 (in Japanese with English summary). Issued also as Transl.Ser.Fish.Mar.Serv.Can., (812)

Hirano, T., 1969 An estimation on distribution of fish eggs and larvae drifted by the Kuroshio Current. Bull.Tokai Reg.Fish.Res.Lab., (44) (in Japanese with English summary)

Hokkaido Fisheries Experimental Station, 1964 Species of octopuses and life of *Paroctopus dofleini* (Wulker) in the coast of Rumoi. Mon.Rep.Hokkaido Fish.Exp.Stn., 21(4-5) (in Japanese)

Honda, S., 1978 Results on the tagging experiment of the common squid, *Todarodes pacificus* Steenstrup. Bull.Fukushima Prefect.Fish.Exp.Stn., (5) (in Japanese)

Inoue, K., 1969 Culture of octopuses. Ser.Aquat.Cult.Jap.Assoc.Fish.Resourc.Protect.,(20):50 p. (in Japanese)

Ishii, M., 1977 Studies on the growth and age of the squid, *Ommastrephes bartrami* (Lesueur) in the Pacific off Japan. Bull.Hokkaido Reg.Fish.Res.Lab., (42) (in Japanese with English summary)

Ishii, M. and M. Murata, 1976 Some information on the fishery and the ecology of the squid, *Dorytheuthis bleekeri* Keferstein, in the coastal waters of the Shiribeshi district in Hokkaido. Bull.Hokkaido Reg.Fish.Res.Lab., (41)

Japan, Ministry of Agriculture, Forestry and Fisheries, 1972 Technical conference. Studies on mechanism underlying the fluctuations in the catch, with references to promotion of forecasting of fishing conditions of Japanese common squid, *Todarodes pacificus* Steenstrup. Res.Rep.Minist.Agric.For.Fish.Japan, (57) (in Japanese)

Japan Sea Regional Fisheries Research Laboratory (ed.), Results of cooperative researches
1977 *Todarodes pacificus* in the Japan Sea. Niigata, Japan Sea Regional Fisheries Research Laboratory, 292 p. (in Japanese)

__________, Report of the symposium on fisheries and fishing grounds for *Todarodes*
1977a *pacificus* stocks. Current status of *T. pacificus* stocks and other major squids fisheries in Japanese coastal waters. Ser.Stud.Jap.Sea Reg., (1):131 p. (in Japanese)

Kaga, K., On the distribution and movement of common squid fish in the northern part
1971 of Japan. Some problems on the results of tagging experiments and its method. Rep.Fish.Resourc.Invest.Sci.Fish.Agency Jap.Gov., (12) (in Japanese with English summary)

Kanamaru, S. and Y. Yamashita, The fishery biology for the octopus, "Mizu-dako" *(Paroctopus*
1969 *hongkongensis* (Hoyle). 1. Summer movements in Onishika area of northwestern part of Hokkaido. Bull.Hokkaido Reg.Fish.Res.Lab., (35) (in Japanese with English summary)

Kasahara, S. and S. Ito, Studies on the migration of common squids in the Japan Sea.
1968 2. Migration and some biological aspects of common squids having occurred in the offshore regions of the Japan Sea during the autumn season of 1966 and 1967. Bull.Jap.Sea Reg.Fish.Res.Lab., (20) (in Japanese with English summary)

Kasahara, S., *et al.*, Contributions of biological information useful for development
1978 of inshore squid fishery in the Japan Sea. 2. A note on reproduction and distribution of *Berryteuthis magister* (Berry) assumed from biological observations on trawl catches in the waters around the Oki Islands, Japan Sea. Bull.Jap.Sea Reg.Fish.Res.Lab., (29) (in Japanese with English summary)

Kawana, K., Y. Takemura and T. Yamane, Tagging experiments of the common squid along the
1970 coast of the Izu Peninsula. Bull.Talai Reg.Fish.Res.Lab., (63) (in Japanese with English summary)

Kawasaki, T., Periodicity in the fluctuation of the fisheries resources. Mar.Sci.Kaivo
1973 Shuppan Co., (10) (in Japanese with English summary)

Kubota, S., *et al.*, Fishery biology on flying squid, *Ommastrephes bartrami* (Lesueur).
1979 2. Analysis of the mantle length distribution of the squid sampled in 1977 fishing season. Bull.Tohoku Reg.Fish.Res.Lab., (41) (in Japanese with English summary)

Machinaka, S., *et al.*, Tagging experiments for the common squid *(Todarodes pacificus)* in
1980 the offshore areas of the Japan Sea, with estimation of parameters in dynamics of squid population. Bull.Ishikawa Prefect.Fish.Exp.Stn., (3) (in Japanese with English summary)

Matsui, I., Fishery biology of a squid, *Doryteuthis bleekeri* Keferstein, in the coast
1974 off Fukushima Prefecture. 2. Bull.Fukushima Prefect.Exp.Stn., (2) (in Japanese)

Matsui, I. and T. Kawasaki, Population structure of the common squid, *Todarodes pacificus*
1971 Steenstrup, distributed in the waters off Joban district. Bull.Tokai Reg. Fish.Res.Lab., (64) (in Japanese with English summary)

Murakami, K., Distribution and migration of *Todarodes pacificus* Steenstrup in the waters
1970 south of Kurile Islands. Mon.Rep.Hokkaido Fish.Exp.Stn., 27(7) (in Japanese)

__________, Distribution of squids in the northwest Pacific Ocean *(Gonatopsis borealis*
1975 Sasaki, *Onychoteuthis borealijaponica* Okada, *Todarodes pacificus* Steenstrup, *Ommastrephes bartrami* Lesueur). J.Hokkaido Fish.Exp.Stn., 33(1) (in Japanese)

Murakami, K., Y. Watanabe and J. Nakata, Growth, distribution and migration of flying
1981 squid *(Ommastrephes bartrami)* in the north Pacific. Res.Inst.North Pac. Fish., Special vol. (in Japanese with English summary)

Murata, M. and H. Araya, Ecological studies on squid, *Todarodes pacificus* Steenstrup,
1970 in the waters off the northeast coast of Hokkaido in 1968. Bull.Hokkaido Reg.Fish.Res.Lab., (36) (in Japanese with English summary)

Murata, M. and M. Ishii, Some information of the ecology of the oceanic squid, *Ommastrephes*
1977 *bartrami* (Lesueur) and *Onychoteuthis borealijaponica* Okada, in the Pacific Ocean off northeastern Japan. Bull.Hokkaido Reg.Fish.Res.Lab., (42) (in Japanese with English summary)

Murata, M., M. Ishii and H. Araya, The distribution of the oceanic squid, *Ommastrephes*
1976 *bartrami* (Lesueur), *Onychoteuthis borealijaponica* Okada, *Gonatopsis borealis* Sasaki and *Todarodes pacificus* Steenstrup in the Pacific Ocean off northeastern Japan. Bull.Hokkaido Reg.Fish.Res.Lab., (41) (in Japanese with English summary)

Murata, M., M. Ishii and M. Osako, On the regeneration of tentacle of the oceanic squid,
1981 *Ommastrephes bartrami* (Lesueur). Bull.Hokkaido Reg.Fish.Res.Lab., (46) (in Japanese with English summary)

Naito, M., K. Murakami and T. Kobayashi, Growth and food habit of oceanic squids
1977 *(Ommastrephedes bartrami, Onychoteuthis borealijaponica, Berryteuthis magister* and *Gonatopsis borealis)* in western sub-Artic Pacific region. Res.Inst.North Pac.Fish., Special volume, December 1977

Naito, M. *et al.*, Distribution and migration of oceanic squids *(Ommastrephes bartrami,*
1977 *Onychoteuthis borealijaponica, Berryteuthis magister* and *Gonatopsis borealis)* in the western sub-Artic Pacific region. Res.Inst.North Pac.Fish., Special volume, December 1977 (in Japanese with English summary)

Nazumi, T., Notes on the species of squids, collected in the Tajima region of the Japan
1975 Sea, 1974. Bull.Hyogo Prefect.Fish.Exp.Stn., (15) (in Japanese)

____________, Notes on the fishery and the ecology of the squid, *Thysanoteuthis rhombus*
1975a Troschel, in the east Sanin water. Bull.Hyogo Prefect.Fish.Exp.Stn., (15) (in Japanese)

Nazumi, T., S. Uota and M. Ogura, Fishing efficiency of incandescent lamp and mercury
1975 lamp in squid fishing. Bull.Hyogo Prefect.Fish.Exp.Stn., (15) (in Japanese)

Okiyama, M. On the feeding habit of the common squid, *Todarodes pacificus* Steenstrup,
1965 in the offshore region of the Japan Sea. Bull.Jap.Sea Reg.Fish.Res.Lab., (14) (in Japanese with English summary)

Okutani, T., Studies on early life history of decapodan Mollusca. 3. Systematics and
1968 distribution of larvae of decapod cephalopods collected from the sea surface on the Pacific coast of Japan, 1960-65. Bull.Tokai Reg.Fish.Res.Lab., (55)9-5

____________, Studies on early life history of decapodan Mollusca. 4. Squid larvae
1969 collected by oblique hauls of a larva net from the Pacific coast of eastern Honshu during the winter seasons of 1965-68. Bull.Tokai Reg.Fish.Res.Lab.,(74)

____________, Stock assessment of cephalopod resources fished by Japan. FAO Fish.Tech.
1977 Pap., (173):62 p.

____________, Illustrated encyclopedia of the useful squids in the world. Tokyo. Towa
1977a Electrical Manufacturing Co., 166 p. Rev.ed. (in Japanese)

Okutani, T. and T. Watanabe, A review of studies on Rhynchoteuthion larva of *Todarodes*
1977 *pacificus*. Mar.Sci.Kaiyo Shuppan Co., 9(4) (in Japanese with English summary)

Research Division, Fishery Agency of Japan, Major fishery resources in Japanese coastal
1972 waters. Tokyo, Fishery Agency, Research Division, 189 p. (in Japanese)

__________, Catch and biological character of fishes caught by Japanese fisheries. (1)
1979 (in Japanese)

Sakurai, M., *et al.*, Fish and fisheries in Kushiro. Kushiro-Ser.Kushiro Munic.Off.,
1972 (13):172-81 (in Japanese)

Sasaki, M., A monograph of the dibranchiate cephalopods of the Japanese and adjacent
1929 waters. J.Fac.Agric.Hokkaido Imp.Univ., (20) Suppl: 357 p.

Sato, T. and H. Hirakawa, The ecological studies on the coho salmon in the northwestern
1978 Pacific Sea. 2. The feature of feeding and morphology. Bull.Conf.Res.N.
Pac., (6) (in Japanese)

Shojima, Y., The common squid, *Todarodes pacificus*, in the East China Sea. 2. Eggs,
1972 larvae and spawning ground. Bull.Seikai Reg.Fish.Res.Lab., (42) (in Japanese)

Soeda, J., Studies on the ecology and the breeding habits of the squid, *Ommastrephes*
1956 *sloani pacificus* Steenstrup. Bull.Hokkaido Reg.Fish.Res.Lab., (14) (in
Japanese with English summary)

Suzuki, H. An ecological study of Japanese common squid, *Todarodes pacificus* Steenstrup
1980 offshore distribution in the Japan Sea. 2. Bull.Kanagawa Prefect.Fish.Exp.
Stn., (1) (in Japanese with English summary)

__________, Some biological aspects of the common squid, *Todarodes pacificus* Steenstrup,
1980a that comes over to off Jyogashima, Kanagawa Prefecture. 2. (In Japanese with
English summary)

__________, Ecological studies on the oceanic squid, *Ommastrephes bartrami* Lesueur.
1980b 1. Bull.Jap.Soc.Fish.Oceanogr., (36) (in Japanese with English summary)

Suzuki, H. and M. Hamabe, Ecological studies on common squid, *Todarodes pacificus*
1977 Steenstrup, in the offshore area in the Sea of Japan. 1. Bull.Tokai Reg.
Fish.Res.Lab., (86) (in Japanese with English summary)

Suzuuchi, T., Results of investigations of stomach contents of *Todarodes pacificus* (Steenstrup)
1974 in the coast of Hakodate. Mon.Rep.Hokkaido Fish.Exp.Stn., 31(2) (in Japanese)

Takeuchi, I., Food animals collected from the stomach of three salmonid fishes
1972 *(Oncorhynchus)* and their distribution in the natural environments in the
northern North Pacific. Bull.Hokkaido Reg.Fish.Res.Lab., (38) (in Japanese
with English summary)

Tashiro, M., Investigations on a species of squidfish, *Loligo edulis edulis*, in the east
1979 China Sea. Bull.Nagasaki Prefect.Inst.Fish., (5) (in Japanese)

Tashiro, M., M. Tateishi and T. Yada, Migration of the squid, *Doryteuthis kensaki*,
1976 obtained from the tagging experiments. Bull.Nagasaki Prefect.Inst.Fish.,
(2) (in Japanese)

Tashiro, M., Y. Yamagishi and T. Suzuuchi, Results of the tagging experiments of a
1972 common squidfish, *Todarodes pacificus* Steenstrup, made in offshore area of
the northern Japan Sea during the summer season of 1970. Sci.Rep.Hokkaido
Fish.Exp.Stn., (14) (in Japanese with English summary)

Tomiyama, A., Ecological studies on the useful sea animals of Yamaguchi Prefecture Inland
1953 Sea. 17. On the cuttlefish, *Sepia esculenta* Hoyle. J.Yamaguchi Prefect.Naikai
Fish.Exp.Stn., 9(1) (in Japanese)

Toyama Fisheries Experiment Station, Mechanism of immigration and utilization of *Watasenia*
1977 *scintillans* (Berry) in the Japan Sea. Toyama, Toyama Fisheries Experiment
Station (mimeo) (in Japanese)

Watanabe, T., Ecological distributions of rhynchoteuthion larva of common squid, *Todarodes*
1965 *pacificus* Steenstrup in the southwest waters off Japan during the winters 1959-62. Bull.Tokai Reg.Fish.Res.Lab., (43) (in Japanese with English summary)

Yamaguchi, K., History of Japanese fishery. Tokyo University Shupankai, 351 p. (in
1957 Japanese)

Yamaguchi Inland Sea Fisheries Experimental Station, Results of researches of Inland
1961 Sea Fisheries Experimental Station in Yamaguchi Prefecture. Result.Res.Inland Sea Fish.Exp.Stn.Yamaguchi Prefect., 11(1) (in Japanese)

Yamamoto, T., Observations on the habits of the squid larvae, *Sepia esculenta* Hoyle, with
1941 special reference to the change of colour pattern on the mantle. Bot.Zool., 9(3) (in Japanese)

__________, Embryonal development of *Sepia esculenta* Hoyle. Bot.Zool., 10(2) (in
1942 Japanese)

Yamashita, Y., On the spawning and hatching eggs of the *Paroctopus dofleini* (Wulker).
1974 J.Hokkaido Fish.Exp.Stn., (Hokusuishi Geppo), 31(7) (in Japanese)

Yasuda, J., Some ecological notes on the cuttlefish, *Sepia esculenta* Hoyle. Bull.Jap.
1951 Soc.Sci.Fish., 16(8) (in Japanese with English summary)

ACKNOWLEDGEMENTS

The authors would like to express our hearty thanks to FAO for giving us an opportunity to present a report on the conditions of the Japanese cephalopod fishery. It is our sincere hope that this report will be of some help to the objectives of the Organization. We are also grateful to Dr H. Araya, Head of Resources Division of Hokkaido Regional Fisheries Research Laboratory, Fisheries Agency for his instructive advice and review of the manuscript and to the members of the Third Laboratory of the Resources Division for their aid in preparing a number of tables and figures.

Table 1

Cephalopod catches in Japan and the world based on FAO statistics (in '000 t)

Year	World total				Japan				Japanese catches from long-distance waters			
	Cuttlefishes	Squids	Octopuses	Total	Cuttlefishes	Squids	Octopuses	Total	Cuttlefishes	Squids	Octopuses	Total
1948	(25)	(320)	(36)	(381)								
49	(23)	(280)	(34)	(337)								
50	(31)	(485)	(41)	(557)								
51	(30)	(545)	(44)	(619)								
52	(37)	680	(54)	(771)		656	37	694				
53	(34)	497	(58)	(589)		468	42	510				
54	(31)	464	(60)	(555)	14	429	43	487				
55	(30)	475	(63)	(568)	13	421	48	482				
56	(34)	396	(64)	(494)	19	336	47	401				
57	(36)	472	(70)	(578)	15	404	52	470				
58	42	462	70	574	19	393	49	461				
59	46	605	71	722	19	519	51	589				
60	44	605	76	725	19	522	58	599				
61	44	568	80	692	20	424	57	501				
62	50	698	93	481	24	579	62	664				
63	43	820	88	951	15	632	57	704				
64	58	453	102	613	23	306	67	396				
65	96	609	150	856	20	441	46	577	29	10	33	72
66	89	596	148	833	15	437	43	551	27	6	23	56
67	101	689	182	972	16	537	43	695	36	9	55	100
68	99	921	193	1 211	15	721	38	876	30	7	65	102
69	101	711	169	981	17	533	41	682	29	11	52	92
70	100	670	161	931	15	490	46	615	17	18	51	86
71	110	630	158	898	15	430	48	568	21	17	38	76
72	139	785	199	1 123	15	541	42	666	25	23	25	73
73	159	715	176	1 051	12	416	43	550	24	35	21	80
74	174	689	211	1 074	17	389	49	547	17	50	28	95
75	184	773	230	1 187	16	469	49	612	11	39	25	75
76	197	764	209	1 173	20	433	42	569	11	33	25	69
77	223	782	190	1 194	20	411	41	580	10	48	27	76
78	231	861	193	1 285	19	440	46	585	6	56	20	82

Note: Data from 1948 to 1964 : Yearbook of fishery statistics (FAO), Vol.22.
Data from 1965 to 1969 : " Vol.36
Data from 1970 to 1973 : " Vol.40
Data for 1974 : " Vol.44
Data from 1975 to 1978 : " Vol.46

Table 2

Cephalopod catches in Japan, 1932-79 (t)

Year	*T. pacificus*a/	Cuttlefish	Other decapodes	Subtotal	Octopods	Total
1932	103 137					
33	114 738					
34	98 422					
35	41 127					
36	71 099					
37	53 558					
38	105 862					
39	126 849					
40	133 571					
41	172 894					
42	125 802					
43	155 349					
44	102 570					
45	108 496					
46	129 149					
47	141 887					
48	301 329					
49	257 463					
50	468 603					
51	595 658					
52	600 870	-	55 571	656 441	37 474	693 915
53	420 086	-	47 839	467 925	41 940	509 865
54	398 745	14 310	30 244	443 299	43 823	487 122
55	383 419	13 481	37 470	434 370	47 629	481 999
56	299 486	18 844	36 113	354 443	47 040	401 483
57	364 365	14 816	39 251	418 432	52 039	470 471
58	354 225	19 115	38 770	412 110	48 968	461 078
59	480 667	19 277	38 329	538 273	50 754	589 027
60	480 661	19 116	41 736	541 513	57 601	599 114
61	383 993	19 845	40 194	444 032	56 857	500 889
62	536 470	23 735	42 348	602 553	61 853	664 406
63	590 647	14 937	41 231	646 815	56 903	703 718
64	238 290	23 216	67 868	329 374	66 975	396 349
65	396 902	20 394	82 071	499 367	78 057	577 424
66	382 899	15 421	86 707	485 027	65 551	550 578
67	477 012	15 736	104 100	596 848	98 130	694 978
68	668 364	15 348	90 065	773 777	102 718	876 495
69	478 160	16 465	95 173	589 798	92 418	682 216
70	412 240	14 740	91 937	518 917	96 127	615 044
71	364 349	15 413	102 756	482 518	85 507	568 025
72	464 365	15 090	119 995	599 450	66 857	666 307
73	347 566	12 225	126 496	486 287	63 764	550 051
74	335 018	17 190	117 759	469 967	76 731	546 698
75	385 255	15 517	137 066	537 838	73 962	611 800
76	312 144	19 750	169 975	501 869	66 873	568 742
77	264 239	20 415	227 925	512 579	67 913	580 492
78	198 516	18 762	302 469	519 747	65 441	585 188
79	212 841	14 137	301 853	528 831	51 986	580 817

a/ After 1978 the catches, by trawling and angling, from the other areas than Japanese coastal waters (New Zealand and Tasmanian waters, etc.), were excluded and included in the statistical category of "Other decapods".

Table 3

Annual landings of *Ommastrephes bartrami* (Lesueur) (t)

Year	Landings a/			Estimated landings by gear	
	Raw	Frozen	Total	Angling	Drift gillnet
1975	20 176	20 988	41 164	41 164	0
1976	31 035	53 145	84 180	84 180	0
1977	29 813	91 955	121 768	121 768	0
1978	52 939	98 369	151 308	100-110 x 10^3	40-50 x 10^3
1979	30 785	93 867	124 652	70-80 x 10^3	40-50 x 10^3
1980	10 745	133 546	144 291	69 105	75 186
	(10 745)	(177 155)	(187 900)	(69 105)	(118 795)

a/ The landings during 1980 include "Tsubonuki" (processed individuals removed head, arms and viscera) as well as round individuals.
Figures in the parentheses are estimated round weight by the following assumption:

(i) All the landings of a raw are made by angling and not included in "Tsubonuki".

(ii) 43.7 percent and 56.3 percent of frozen landings are made by angling and drift gillnet respectively.

(iii) All the landings by angling are on the raw basis.

(iv) All the landings by drift gillnet consist of 41.2 percent of raw and 58.4 percent of "Tsubonuki".

(v) Conversion factor: Round weight = "Tsubonuki" x 2.0

Table 4

Cephalopods commercially taken in Japan
(including those taken incidentally in fisheries for other species)

Family	Species	Locality	Gears[a]
Sepiidae	*Sepia lycidas* Gray	S.W. Japan, E. China Sea	TR, FN, AJ
	S. esculenta Hoyle	whole Japan excluding N. Hokkaido	TR, FN, AJ
	S. latimanus Quoy and Gaimard	Amami-Okinawa	SP, AJ
	S. madokai Adam	W. Japan, Inland Sea	TR
	S. lorigera Wulker	W. Japan, Inland Sea	TR
	S. andreana Steenstrup	N.E. Japan	TR, FN
	Sepiella japonica Sasaki	W. Japan, E. China Sea	TR
Sepiolidae	*Rossia pacifica* Berry	N.E. Japan	TR
	Euprymna morsei Verrill	Inland Sea	TR
Loliginidae	*Sepioteuthis lessoniana* Lesson	Whole Japan, excluding N. Hokkaido	FN, AJ
	Doryteuthis bleekeri (Keferstein)	Whole Japan, excluding N. Hokkaido	TR, FN, AJ
	Loligo edulis Hoyle	W. Japan	TR, FN, AJ
	L. edulis budo Wakiya and Ishikawa	Japan Sea	TR, FN
	L. japonica Hoyle	Whole Japan, excluding N. Hokkaido	FN, BS
	L. beka Sasaki	Inland Sea, W. Kyushu	FN, TR, BS
	L. kobiensis Hoyle	Inland Sea, Kyushu	FN, TR, BS
	L. uyii Wakiya and Ishikawa	Inland Sea, Kyushu	TR, FN, BS
Enoploteuthidae	*Watasenia scintillans* (Berry)	Japan Sea (Toyama Bay)	FN
Onychoteuthidae	*Onychoteuthis borealijaponica* Okada	E. Japan	AJ
Gonatidae	*Berryteuthis magister* (Berry)	N. Japan	TR
	Gonatopsis borealis Sasaki	N. Japan	AJ
Ommastrephidae	*Symplectoteuthis oualaniensis* (Lesson)	Okinawa	AJ
	Ommastrephes bartrami (Lesueur)	N.E. Japan (Pacific)	AJ
	Todarodes pacificus Steenstrup	Whole Japan	AJ, FN, TR
Thysanoteuthidae	*Thysanoteuthis rhombus* Troschel	Japan Sea	AJ
Octopodidae	*Octopus vulgaris* (Lamarck)	Whole Japan, excluding Hokkaido	OP, AJ
	O. ocellatus Gray	W. Japan	OP
	O. minor Sasaki	Inland Sea, W. Japan	TR, OP
	O. conispadiceus Sasaki	Hokkaido	TR, OP
	O. araneoides Taki	Hokkaido	TR, OP
	Octopus dofleini (Wulker)	N.E. Japan	TR, OP

[a] AJ: angling and jigging; BS: boat seines; FN: fixed (stationed) net; OP: octopus pot (trap); SP: spearing; TR: trawling (of various scales)
(Okutani, 1977)

Table 5

Annual catches, by fishing gears, of *Todarodes pacificus* from the Japanese coastal waters (t)

Year	Angling	Inshore						Offshore		Other waters and fisheries	Total
		Other Angling	Gillnet	Large trap net	Small trap net	Haul seine	Small trawler	Small trawler[a]	Small trawler[b]		
1952	555 011	435	19	35 333	2,906	64	79	0	1 466	538	595 851
53	394 256	379	56	21 761	968	12	1 729	150	0	709	420 020
54	375 199	1 920	405	14 506	3 811	0	112	360	1 208	659	398 180
55	361 834	3 015	34	10 819	5 093	4	184	315	1 328	627	383 253
56	262 650	2 261	109	27 787	4 181	12	83	334	1 650	319	299 386
57	338 516	251	88	16 136	5 585	67	143	477	2 036	736	364 035
58	336 547	169	154	10 506	3 441	21	222	1 300	1 018	767	354 145
59	455 358	160	127	15 608	6 100	10	277	687	2 378	516	481 221
60	454 030	423	25	16 259	5 528	19	443	559	2 333	837	480 456
61	360 272	289	73	15 138	5 312	57	194	636	1 188	817	383 976
62	513 807	475	63	14 733	4 021	14	267	331	1 742	1 085	536 207
63	566 355	489	66	14 947	4 763	11	175	488	2 082	1 225	590 601
64	215 818	262	29	14 536	5 521	38	165	575	563	708	238 215
65	373 897	351	530	12 637	6 416	11	326	714	1 356	660	396 899
66	362 109	226	127	10 912	6 618	5	312	525	1 350	702	382 886
67	450 921	224	401	11 243	8 270	25	221	525	3 352	1 824	477 006
68	637 118	384	546	9 302	14 364	7	253	589	4 379	1 353	668 295
69	451 895	130	82	8 604	12 405	5 580	398	529	3 735	370	483 728
70	392 257	112	52	9 256	6 207	22	379	669	2 723	539	412 216
71	347 986	98	26	6 372	3 270	10	480	4	5 692	394	364 332
72	442 852	134	42	5 325	4 562	17	487	32	10 583	170	464 204
73	332 884	115	45	6 090	2 146	20	446	1 339	3 822	610	347 527
74	318 351	234	46	4 033	2 849	28	489	1 020	7 716	215	334 981
75	361 119	219	58	4 495	1 643	19	1 027	1 619	7 272	449	377 920
76	293 000	403	5	2 895	1 282	51	736	2 879	2 210	150	303 611
77	223 000	307	120	4 231	1 532	39	1 584	936	2 438	232	234 419
78	189 692.	328	1 032	2 497	874	18	890	1 206	1 836	143	198 516
79	202 301	136	188	2 170	611	29	1 618	1 997	3 758	32	212 846

Note :

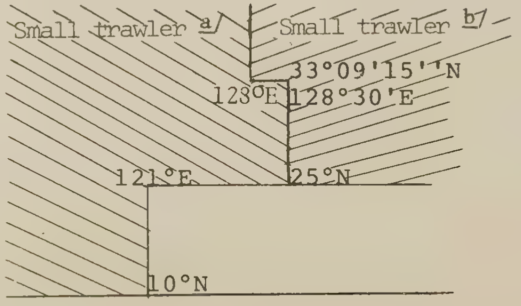


Table 6

Annual catches, by fishing gears, of cuttlefishes from the Japanese coastal waters (t)

Year	Angling	Inshore						Offshore		Other waters and fisheries	Total
		Miscella. angling	Miscella. longline	Large trap net	Small trap net	Haul seine	Small trawler	Small a/ trawler	Small b/ trawler		
1954	1 534	450	203	180	1 013	664	1 514	6 488	289	1 939	14 274
55	1 999	379	184	221	754	941	2 078	5 171	360	1 362	13 449
56	2 138	664	304	424	1 714	420	2 577	7 171	368	3 056	18 836
57	1 950	236	255	492	574	634	1 959	6 221	263	2 181	14 765
58	2 412	276	359	352	1 361	1 524	2 923	7 432	183	2 280	19 102
59	2 469	226	576	294	1 295	1 198	2 792	7 140	144	3 131	19 265
60	2 289	305	659	108	1 040	1 257	2 704	7 883	203	2 655	19 103
61	2 454	218	690	125	897	2 358	2 823	7 972	162	2 132	19 831
62	2 834	211	672	328	1 485	5 592	2 448	7 575	105	2 475	23 725
63	1 269	208	446	245	833	1 838	2 094	5 743	106	2 146	14 928
64	1 183	191	506	114	615	133	2 800	9 489	102	1 895	17 028
65	1 340	203	526	91	545	1 377	2 755	11 309	113	2 134	20 393
66	1 409	171	456	59	412	2 836	3 189	4 971	179	1 741	15 423
67	1 684	242	619	171	1 085	1 962	3 149	4 670	82	2 071	15 735
68	2 560	207	679	845	1 545	2 961	2 797	1 937	48	1 736	15 315
69	1 531	164	668	162	1 381	1 285	2 984	2 259	44	1 588	12 066
70	1 271	171	745	215	1 834	3 617	3 052	1 651	64	2 120	14 740
71	2 833	207	769	456	1 849	3 748	2 840	0	0	2 711	15 413
72	2 160	174	762	245	1 494	2 030	3 535	2 689	0	2 001	15 090
73	1 362	417	775	196	2 093	1 491	3 673	170	203	1 761	12 141
74	3 168	250	1 062	604	1 434	3 026	4 677	265	45	2 638	17 169
75	1 384	225	843	283	1 891	3 680	4 512	517	28	2 153	15 516
76	1 350	237	1 325	380	1 665	6 850	4 532	500	9	2 772	19 620
77	1 556	140	911	411	2 074	7 895	5 133	319	12	1 957	20 408
78	1 384	261	908	140	1 269	4 097	8 246	472	20	2 010	18 807
79	542	250	1 149	163	1 001	1 628	7 137	382	23	1 855	14 130

a/ b/ See footnote on Table 5

Table 7

Catches of decapods (excluding *Todarodes pacificus* and cuttlefishes), by gears, from Japanese coastal waters (t)

Year	Angling	Inshore						Offshore		Other waters and fisheries	Total
		Miscella. angling	Miscella. gillnet	Large trap net	Small trap net	Haul seine	Small trawler	Small[a/] trawler	Small[b/] trawler		
1952	11 846	1 013	251	7 380	2 618	1 125	3 612	15 233	5 021	2 581	50 680
53	10 943	1 110	233	6 968	3 342	1 264	7 951	13 579	0	2 420	47 810
54	5 891	368	222	4 373	5 495	375	1 549	9 450	1 371	588	30 182
55	9 668	525	146	4 148	4 995	395	1 856	11 011	2 921	991	36 656
56	8 809	529	105	4 294	5 063	484	1 759	10 921	2 966	1 138	36 068
57	11 558	360	165	4 822	6 784	450	1 868	9 421	2 280	1 487	39 195
58	13 440	402	171	3 735	4 488	446	2 183	10 115	2 474	1 342	38 796
59	12 198	429	179	3 675	4 519	412	2 363	10 932	2 036	1 576	38 319
60	13 299	469	227	4 734	5 234	374	2 058	10 967	2 746	1 612	41 720
61	14 503	426	254	4 370	4 948	291	2 322	9 720	1 585	1 759	40 178
62	16 077	577	271	3 568	5 372	374	2 615	9 399	2 285	1 792	42 330
63	12 037	593	235	4 020	7 125	695	2 786	10 090	1 848	1 308	40 737
64	19 754	569	264	4 815	7 285	463	3 876	13 738	1 784	1 158	53 706
65	11 226	482	333	3 567	6 500	286	3 927	13 210	2 538	1 398	43 467
66	14 400	379	303	3 491	5 953	533	3 910	21 737	1 599	1 347	53 652
67	18 859	570	497	4 687	5 890	1 053	4 046	21 062	1 928	1 307	59 899
68	9 181	776	585	3 282	5 411	1 879	3 310	24 648	2 127	1 405	52 604
69	13 730	603	467	3 165	4 818	848	4 389	21 967	2 115	1 071	53 173
70	9 764	448	495	4 370	5 485	1 069	5 031	24 392	4 684	940	56 678
71	13 356	530	406	3 569	7 410	849	5 297	32 211	628	1 295	65 551
72	20 255	728	497	5 910	9 432	481	5 004	30 323	487	851	73 968
73	18 784	508	465	6 300	8 713	488	5 617	34 035	4 526	1 376	80 812
74	25 425	607	556	3 609	7 799	1 029	5 754	27 428	4 275	1 257	77 739
75	46 439	880	612	3 884	7 609	870	6 169	34 909	3 204	958	105 534
76	85 240	560	642	4 788	7 474	5 066	5 825	31 896	3 086	1 268	145 845
77	121 477	798	521	6 701	7 295	958	6 668	48 538	5 169	1 253	199 378
78	131 313	843	25 280	4 630	7 439	926	7 371	37 660	5 047	1 532	222 041
79	130 342	655	33 955	5 320	7 536	563	6 718	39 175	7 755	634	232 653

a/ b/ See footnote on Table 5

Table 8

Annual catches of octopods, by fishing gears, from the Japanese coastal waters (t)

Year	Offshore	Inshore								Other waters and fisheries	Total
	Small[a/] trawler	Miscella. angling	Miscella. longline	Miscella. gillnet	Large trap net	Small trap net	Haul Seine	Small trawler	Miscella. fisheries		
1952	7 661	4 320	9 994	165	30	109	2 610	113	11 010	178	36 190
53	0	4 680	13 335	203	11	154	0	10 962	12 311	162	41 818
54	8 539	4 628	14 745	101	4	199	1 789	529	12 806	196	43 536
55	8 929	7 826	13 189	175	8	210	2 809	544	1 357	212	35 259
56	8 370	5 921	13 744	244	30	244	2 907	386	14 659	410	46 915
57	9 064	5 584	16 001	323	4	188	4 166	334	15 814	413	51 891
58	8 295	5 882	14 266	313	3	207	4 112	410	14 739	611	48 838
59	8 000	6 144	14 423	323	23	167	4 330	321	16 355	539	50 625
60	8 352	7 520	15 711	295	17	184	5 388	270	19 150	591	57 478
61	6 929	8 467	12 222	341	10	199	5 569	176	22 295	512	56 720
62	7 547	8 852	12 401	882	22	239	7 051	108	23 976	625	61 703
63	5 226	7 047	13 408	304	12	151	5 570	71	24 127	765	56 681
64	5 531	6 370	12 775	490	9	256	6 770	39	23 824	246	56 310
65	4 777	4 334	11 375	434	23	203	6 781	40	16 224	327	44 518
66	3 629	3 867	10 260	477	18	213	6 364	30	17 649	286	42 793
67	3 455	3 859	9 030	619	59	261	8 281	14	16 868	312	42 758
68	3 584	2 939	7 529	554	44	203	7 541	19	14 871	444	37 728
69	3 733	2 910	6 568	731	54	277	9 341	11	15 968	414	40 007
70	3 893	2 471	9 335	825	36	326	9 105	19	18 879	257	45 146
71	3 122	2 579	11 302	776	46	310	8 950	22	20 223	42	47 372
72	3 039	2 296	6 407	677	37	365	9 089	74	19 451	70	41 505
73	2 461	2 265	7 784	712	38	321	9 413	10	19 701	99	42 804
74	2 454	2 802	9 017	839	23	351	10 305	58	22 477	184	48 510
75	2 382	2 475	8 129	795	31	432	12 400	20	22 537	151	49 352
76	1 917	2 294	5 808	1 077	83	453	10 085	45	20 177	170	42 109
77	2 310	1 822	4 925	969	47	506	8 058	21	21 549	190	40 397
78	2 616	1 663	7 205	1 190	41	571	9 767	63	22 024	176	45 316
79	3 177	1 396	6 200	1 166	34	508	9 546	18	19 477	198	41 720

a/ See footnote on Table 5

Table 9

Annual catches of *Todarodes pacificus*, by areas, from the waters off northern Japan (t)

Year	Pacific off northern Japan				Sea of Japan off northern Japan				Total
	Norhteastern Hokkaido	Southern Hokkaido	Northern Honshu	Subtotal	Western Hokkaido	Coast of Honshu	Offshore of Sea of Japan	Subtotal	
1932									103
33									115
34									98
35									41
36									71
37									54
38									106
39									127
40									134
41									173
42									126
43									155
44									103
45									108
46									129
47									142
48									301
49									257
50									469
51									517
52	15	272	155	442	61	44	0	105	596
53	39	172	138	349	18	28	0	46	420
54	29	180	98	307	50	28	0	78	398
55	25	170	124	319	23	22	0	45	383
56	36	84	121	241	29	16	0	45	299
57	45	97	123	265	33	41	0	74	364
58	110	43	102	255	40	37	0	77	354
59	113	99	161	373	46	33	0	79	481
60	150	75	146	371	31	25	0	56	480
61	119	69	103	291	29	27	0	56	384
62	211	54	193	458	27	20	0	47	536
63	212	55	167	434	47	38	0	85	590
64	64	52	45	161	30	41	0	71	238
65	214	39	69	322	41	39	0	80	397
66	135	47	83	265	34	48	3	82	383
67	236	62	97	395	39	39	7	85	477
68	329	69	95	493	64	42	15	121	668
69	221	57	59	337	21	27	42	90	483
70	87	53	38	179	56	67	73	196	412
71	40	42	30	112	49	23	114	186	364
72	98	37	37	172	87	29	179	296	464
73	9	26	7	38	75	33	168	276	348
74	14	22	12	48	61	26	161	248	335
75	27	35	16	77	45	32	161	238	378
76	+	8	1	10	43	49	139	231	304
77	1	4	1	7	32	39	82	153	234
78	+	3	1	4				(148)	199
79	+	2	1	3				(154)	213

Note: 1. Catches in Pacific and in Sea of Japan off northern Japan are based on the data from Hokkaido Reg. Fish. Res. Lab., Japan Sea Fish. Res. Lab., and Pre. Fish. Exp. Stations
2. Total catches are based on Annual Report of Statistics of Fisheries and Culture Production, Min. Agr. For. and Fish., Japan.
3. Therefore, total catches are not equal to the total of catches in Pacific and in Sea of Japan.
4. ( ):Estimated

Table 10

Number of boats for squids angling fishery

Year	Non-powered boats	Powered boats							
		Under 3 t	3-5 t	5-10 t	10-20 t	20-30 t	30-50 t	50-100 t	100-200 t	Over 200 t
1958	19 817	19 499	1 860	1 256	1 247	258	181	25	2	
59	18 606	20 756	2 093	1 281	1 389	213	225	51	1	
60	16 235	22 672	2 190	1 217	1 252	283	224	14	-	
61	15 106	23 672	2 365	1 270	1 249	358	273	33	2	
62	11 919	22 938	2 656	1 319	1 141	383	373	50	4	
63	8 626	21 848	2 802	1 311	1 091	350	440	93	4	
64	7 513	21 715	3 119	1 305	1 150	343	418	124	7	
65	6 128	22 695	3 460	1 415	1 274	406	484	202	6	
66	4 842	23 340	3 982	1 508	1 361	332	503	255	5	
67	4 059	23 637	4 136	1 559	1 359	337	579	318	9	
68	2 785	21 610	4 339	1 687	1 391	336	639	377	8	
69	2 395	21 900	4 875	1 669	1 423	367	711	509	2	16
70	2 060	21 523	5 382	1 851	1 423	309	741	803	8	53
71	1 544	21 183	5 572	1 953	1 514	285	696	985	11	75
72	1 152	19 952	6 203	2 153	1 669	273	830	1 402	41	100
73	889	19 782	6 476	2 177	1 624	217	677	1 417	37	97
74	561	20 657	7 021	2 298	1 654	162	636	1 196	50	127
75	335	20 245	7 938	2 640	1 743	138	595	1 243	51	140
76	223	18 238	8 101	2 689	1 839	117	514	1 184	56	146
77	213	19 405	9 194	2 970	1 941	108	498	1 195	58	168
78	126	19 147	8 966	3 027	2 002	85	469	1 298	44	192
79	114	19 353	10 038	3 208	2 124	80	458	1 337	44	195

Table 11

Catch per fishing day for decapods angling fisheries by size of boats[a] (kg)

Year	Non-powered boats	Powered boats								
		Under 3 t	3-5 t	5-10 t	10-20 t	20-30 t	30-50 t	50-100 t	100-200 t	Over 200 t
1958	15	58	226	632	1 701	2 156	2 618	3 472		
59	14	62	268	938	1 924	3 122	3 529	4 068		
60	18	64	289	639	2 156	3 475	3 702	5 032		
61	21	63	225	555	1 411	2 377	2 634	3 025		
62	25	64	192	698	1 534	3 157	3 756	2 981		
63	10	102	328	660	1 347	2 649	3 229	3 025		
64	10	54	141	289	627	1 218	1 027	1 716		
65	9	56	146	429	863	2 046	2 093	2 374		
66	7	52	127	353	643	1 674	1 780	1 896		
67	8	54	146	405	631	1 803	1 960	2 614		
68	8	71	194	445	741	2 747	2 602	2 710		
69	10	43	120	261	502	1 455	1 733	1 746		3 160
70	10	42	108	234	362	934	1 262	1 314		1 474
71	17	35	83	182	248	648	806	1 146	1 231	1 634
72	11	29	81	211	336	695	756	998	1 644	1 414
73	9	25	62	149	220	433	586	859	1 421	1 489
74	13	23	55	158	217	408	563	810	1 047	1 115
75	6	22	63	179	240	688	692	848	1 165	1 288
76	6	20	59	163	199	455	607	815	1 321	1 390
77	6	17	41	125	161	467	543	710	1 761	1 773
78	4	16	42	124	209	346	615	772	1 434	2 004
79	4	16	39	115	218	362	590	731	1 020	1 393

---

[a] All species combined

Table 12

Catch-per-day-per-boat for *Ommastrephes bartrami* fisheries by size of boats and month (t)

Year	Tonnage	Gear	July	Aug.	Sep.	Oct.	Nov.
1978	Under 30	A	-	1.6	1.3	1.9	-
		D	-	-	3.2	2.8	3.0
	30-99 t	A	2.1	2.3	2.2	1.5	1.3
		D	-	-	-	4.0	5.0
	Over 100 t	A	1.6	2.9	2.1	2.2	2.8
		D	-	-	-	-	-
1979a/	30-99 t	A	0.5	1.8	2.2	1.8	1.7
		D	4.0	4.3	6.7	6.8	5.9
	Over 100 t	A	0.8	2.5	2.7	1.8	0.6
		D	4.2	4.9	5.1	4.9	4.1

A : Angling
D : Drift gillnet

a/ Location of fishing grounds is different between angling and drift gillnet
Data frozen landings only.

Table 13

Annual catches of cuttlefishes by area (t)

Year	Hokkaido	Pacific			Sea of Japan			Seto Inland Sea	Total
		Off northern Japan	Off central Japan	Off southern Japan	Off northern Japan	Off western Japan	Off western Kyushu		
1965	-	80	237	1 413	79	2 008	10 263	6 314	20 394
66	-	55	295	1 155	59	1 556	4 490	7 810	15 421
67	-	58	249	1 492	95	1 984	4 421	7 437	15 736
68	-	35	200	2 819	43	1 774	1 744	8 733	15 348
69	270	22	141	2 085	49	2 156	1 923	11 014	17 660
70	-	28	181	1 651	14	2 175	2 151	9 402	15 602
71	-	16	138	2 573	17	485	2 333	9 851	15 413
72	-	9	88	2 394	130	3 036	1 538	7 895	15 090
73	-	43	224	1 652	158	332	2 085	7 647	12 141
74	-	13	196	4 671	87	372	2 163	9 667	17 169
75	-	19	142	2 352	118	348	2 383	10 155	15 517
76	-	9	332	2 684	61	592	2 326	13 746	19 750
77	-	14	201	1 479	575	391	2 327	15 428	20 415
78	-	8	144	1 573	79	400	2 456	14 114	18 762
79	-	27	222	1 082	76	567	2 580	9 582	14 137

Table 14

Annual catches of octopuses by area (t)

Year	Hokkaido	Pacific			Sea of Japan			Seto Inland Sea	Total
		Off northern Japan	Off central Japan	Off southern Japan	Off northern Japan	Off western Japan	Off western Kyushu		
1965	20 159	7 169	19 108	460	1 142	10 194	9 260	10 565	78 057
66	20 751	5 668	14 058	480	1 125	6 936	6 683	9 851	65 551
67	18 567	6 864	32 561	530	2 121	17 209	9 414	10 865	98 130
68	17 821	5 627	38 088	242	2 650	21 748	8 802	7 740	102 718
69	18 450	8 223	1 300	201	1 122	1 108	2 846	7 961	41 211
70	22 469	8 571	1 450	213	1 066	855	2 853	8 620	46 097
71	26 201	6 904	21 664	239	2 313	16 889	2 287	9 010	85 507
72	19 718	7 246	13 037	225	1 970	12 975	2 927	8 759	66 857
73	21 519	8 943	12 042	666	1 403	7 793	2 332	7 580	62 278
74	23 708	7 128	21 559	665	1 802	6 935	5 768	9 166	76 731
75	22 766	8 225	19 339	782	1 241	5 187	5 112	11 310	73 962
76	17 517	6 113	16 747	643	1 595	7 079	6 011	11 168	66 873
77	19 066	5 473	20 594	410	2 202	6 229	7 038	6 901	67 913
78	20 394	6 618	16 338	499	2 181	4 360	5 757	9 293	65 441
79	17 798	7 614	9 457	283	2 049	2 053	4 497	8 236	51 986

Table 15

Annual catches of octopuses[a]

Area		1964	1965	1966	1967	1968	1969	1970	1971	1972	1973
Sea of Japan	Soya	8 496	5 696	7 145	5 804	5 479	5 733	5 336	5 756	3 903	4 392
	Rumoi	3 772	3 652	3 548	2 786	2 788	3 327	3 794	4 079	3 772	4 099
	Ishikari	131	88	88	74	57	53	40	101	60	96
	Shiribeshi	1 478	1 559	1 470	1 253	1 485	1 726	2 615	3 714	2 523	2 853
	Hiyama	362	479	464	592	348	267	413	505	607	435
	Subtotal	14 239	11 474	12 715	10 509	10 157	11 106	12 198	14 155	10 865	11 875
Pacific west of Erimo Cape	Oshima	1 859	1 917	2 101	2 039	1 409	2 159	2 580	2 181	2 463	2 349
	Iburi	288	209	310	403	420	382	467	470	484	356
	Hidaka	2 387	2 216	1 758	1 837	1 789	1 648	2 454	2 227	1 521	2 344
	Subtotal	4 534	4 342	4 169	4 279	3 618	4 189	5 501	4 878	4 468	5 049
Off eastern Hokkaido	Tokachi	753	1 061	976	1 096	257	443	297	523	337	500
	Kushiro	2 143	1 817	1 282	1 560	1 948	1 601	2 850	3 116	2 134	2 050
	Nemuro	777	702	538	341	274	147	625	1 699	773	857
	Subtotal	3 673	3 580	2 796	2 997	2 479	2 191	3 772	5 338	3 244	3 407
Okhotsk Sea	Abashiri	1 153	768	1 071	781	1 006	894	900	1 830	1 141	1 188
Total catches in Hokkaido		23 604	20 163	20 751	18 566	17 260	18 380	22 371	26 201	19 718	21 519
Total Japanese catches		66 975	78 057	65 551	98 130	102 718	92 418	96 127	85 507	66 857	62 278

[a] Data from Yearbook of Agri. Forest and Fish. Statistics in Hokkaido.

Table 16

Annual catches of Loliginid squid in each district of Hokkaido and Aomiri Prefecture in the Japan Sea side [a]

Year	Aomori Prefecture	Oshima Province	Hiyama Province	Shiribeshi Province	Rumoi Province	Soya Province
1955	74	158	668	814	150	0
56	177	413	323	619	106	45
57	111	334	368	540	240	105
58	342	269	132	309	266	165
59	564	421	63	418	264	24
60	331	125	119	1 250	81	24
61	1 196	276	163	400	120	3
62	770	412	194	476	43	153
63	1 016	711	1 037	411	271	194
64	1 200	1 400	200	300	0	0
65	1 633	708	132	171	51	41
66	1 673	485	110	207	140	56
67	966	1 447	162	204	2	0
68	1 224	295	34	54	66	36
69	827	224	78	267	2	-
70	810	186	34	30	4	-
71	2 145	262	54	485	26	-
72	1 811	686	329	451	29	6

Data from Statis.& Infor.Dept.,Minis. of Agri. Forest,& Fish.

[a] Since catch statistics for Loliginid squid alone is not available the nominal statistics in item of "Other Decapods" in which there are little other species than Loliginid squid, if any, are presented in the Table.

Table 17

Annual catches of *Loligo edulis* Hoyle and *L. edulis budo* Wakiya and Ishikawa by type of fisheries

Type of fish.	Trawler-1 (tow boats)		Trawler-2 (tow boats)		Angling		Trap net		Others		Total	
Fishing area	East China Sea		W. Jap. Sea - W. Goto Is.		NW-S of Kyushu		NW-S of Kyushu		NW-S of Kyushu			
Year	Catch (t)	Effort (No. hauls)	Catch (t)	Effort (No. hauls)	Catch (t)	Effort (fish. days)	Catch (t)	Effort (No. nets)	Catch (t)	Effort	Catch (t)	Effort
1968	9 000	610 x 10^3	490	73 223	4 800	670 x 10^3	1 400	1 164	800	-	16 000	-
1969	7 000	580	790	71 929	7 000	840	1 300	1 246	800	-	17 000	-
1970	8 000	540	1 240	66 032	4 100	770	1 500	1 482	800	-	16 000	-
1971	9 000	480	1 850	66 437	5 100	800	1 800	1 478	1 100	-	19 000	-
1972	7 000	400	2 110	67 788	9 300	890	1 900	1 575	1 100	-	21 000	-
1973	7 000	390	1 660	71 135	6 700	800	1 700	1 627	900	-	18 000	-
1974	6 000	360	910	66 142	6 900	790	1 900	1 797	1 200	-	17 000	-
1975	9 000	380	1 073	67 946	8 300	830	1 700	1 791	1 200	-	21 000	-
1976	7 000	390	1 861	70 109	7 700	840	2 000	1 819	800	-	19 000	-
1977	14 000	400	2 599	71 887								
Depth	40-130 m		100-150 m		20-100 m		5-30 m		5-100 m			
Season	Jan.-Dec.		Jan.-May, Aug.-Dec.		Mar.-Dec.		Jan.-Dec..					
Age group	0 age		0 age		0 age		0 age		0 age			

Monthly catches in 1977 (t)

Type of fish.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Total
Trawler-1	900	800	900	600	600	1 300	1 200	1 700	1 600	1 700	1 600	1 100	14 000
Trawler-2	376	202	194	124	87	←off-season→		184	702	468	165	99	2 599
Angling	←off-season→			0.7	11.5	21.5	17.9	19.8	55.4	37.0	6.3	4.4	174
Trap net	1.6	0.1	0.2	1.5	3.6	7.3	5.6	0.2	0.7	1.1	0.5	0.8	23

Data source: Statis. and Infor. Dept., Ministry of Agriculture, Forestry and Fisheries

Table 18

Annual and monthly catches of *Thysanoteuthis rhombus* Troschel in Hyogo Pref. (t)

Year	Catch	Monthly catches					
		July	Aug.	Sep.	Oct.	Nov.	Dec.
1962	2.0						
63	0						
64	232.5						
65	5.0						
66	7.0						
67	619.8	2.0	22.9	48.4	312.4	224.7	9.4
68	0.1						
69	26.7						
70	66.8						
71	62.5						
72	516.0		0.3	131.3	274.3	107.1	3.3
73	305.0		24.9	117.5	114.4	44.2	4.0
74	44.2		0.5	16.6	16.5	9.0	1.6

Table 19

Spawning ground and seas of *Todarodes pacificus* in the Tsushima warm current

Population	Spawning ground	Spawning season
Winter population	Southwestern Japan Sea west of Toyama Bay Area off western Kyushu to edge of continental shelf in the East China Sea	Jan.- Mar. Jan.- Apr.
Summer population	Tobishima to Noto Peninsula Southwestern Japan Sea west of Noto Penin. Eastern coast of Korea Area off western Kyushu to edge of continental shelf in the central East China Sea	July - Sep. June - Aug. June - Aug. May - July
Fall population	Southwestern Japan Sea to northwestern Kyushu Southeastern coast of Korea Edge of continental shelf in the northern and central East China Sea	Sep.- Nov. Sep.- Nov. Oct.- Dec.

Table 20

Fishing ground and season of *Todarodes pacificus* angling in the Japan Sea

Fishing ground	Fishing season	Origin	Stage in life history
1. Inshore			
Western Japan Sea	Apr.-July	sp	pm, m
		wp	im
	Oct.-Nov.	fp	pm, m
	Dec.-Feb.	wp	pm
Northern Japan Sea	May-Aug.	wp	im
		fp	im
	Dec.-Mar.	wp	pm
		sp	im
Western Hokkaido	June-Sep.	wp	im
		fp	im, pm
	Oct.-Dec.	wp	pm
Northern Hokkaido	Aug.-Nov.	wp	im, pm
		fp	pm
Tsushima Strait	Sep.-Nov.	fp	pm, m
	Jan.-Mar.	wp	pm, m
2. Offshore			
Hakusan Shoals	July-Sep.	wp	im
		fp	im, pm
Oki I., Bank	June-Oct.	fp	im, pm
Yamato Bank	July-Sep.	fp	im, pm
Ullung I.	Sep.-Oct.	fp	pm
Takeshima I.	Oct.-Nov.	fp	pm, m
North of Tsushima I.	Oct.-Nov.	fp	pm, m
	Dec.-Feb.	wp	pm, m

sp:	summer population	wp:	winter population	pm:	premature
fp:	fall population	im:	immature	m:	mature

Table 21

Indices of abundance and density of the fall population of *Todarodes pacificus* in the Japan Sea[a/]

Year	Area north of 42°N			Area south of 42°N		
	A	P	f	A	P	f
1971	1,739	100.9	58.0	1,100	40.5	36.8
72	1,664	61.0	36.7	1,100	31.4	28.5
73	1,733	38.5	22.2	1,100	22.9	20.8
74	1,379	32.7	23.6	1,100	27.9	25.4
75	1,498	40.3	26.9	1,099	25.2	22.9
76	1,532	29.6	19.3	1,063	20.6	19.6
77	-	-	-	921	11.4	12.3
78	1,284	19.9	15.5	1,100	14.3	13.0
79	1,272	20.8	16.4	1,100	18.4	16.7
80	1,243	26.5	21.3	1,089	24.7	22.7
81	1,131	14.0	12.4	1,031	13.0	12.6

$P = \Sigma A_i f_i$

P : Index of abundance
A : Index of area
f : Index of density

a/ East of long. 130°-30'E, lat. 36°-42'N for early June and East of long. 130°-30'E, lat. 36°-45°-30'N for August to early September

Table 22

Distribution of *Todarodes pacificus* larvae in fall based on 80-RN net survey

Year	Southwestern Japan Sea	Area around Kyushu	Whole area
(A)			
1973	0.59	-	-
74	0.32	0.82	0.53
75	0.73	0.53	0.66
76	0.52	0.62	0.57
77	0.37	0.29	0.33
78	0.21	0.46	0.33
79	0.55	0.48	0.51
80	0.60	0.74[a]	0.64[a]
(B)			
1973	12.71	-	-
74	2.68	8.31	6.38
75	13.16	7.75	11.69
76	5.12	2.48	3.80
77	5.57	1.61	3.83
78	1.92	1.79	1.83
79	3.50	1.50	2.61
80	4.43	5.24[a]	4.73[a]
(C)			
1973	1.82	-	-
74	0.46	2.22	1.21
75	2.27	1.28	1.94
76	1.08	0.95	1.02
77	0.66	0.35	0.51
78	0.28	0.58	0.43
79	0.93	0.57	0.76
80	1.14	1.51[a]	1.26[a]
(D)			
1973	749.9	-	749.9
74	85.7	681.4	767.1
75	960.7	410.8	1 371.5
76	266.4	153.8	2 817.8
77	206.1	46.7	252.8
78	40.3	82.3	122.6
79	192.5	72.0	264.5
80	265.8	111.7	377.5

[a] Preliminary

A : s/S
B : n/s
C : $\Sigma\sqrt{n}/S$
D : A·B·100

S : Number of stations towed plankton net
s : Number of stations at which larvae occured
n : Number of larvae

Table 23

Numbers of fishing days (N), catch in case per fishing day (CPUE 1), and catch in number per fishing day (CPUE 2) by jigging boats of Aomori Prefecture for *Ommastrephes bartrami*[a]

		1976	1977	1978	1979	1980
N	Boats in 30-99 tons[b]	7 722	10 492	16 185	11 568	3 025
	Boats over 100 tons	2 756	4 697	7 812	7 125	6 400
	Total	10 478	15 189	23 987	18 693	9 425
CPUE 1	Boats in 30-99 tons[b]	191	216	139	147	191
	Boats over 100 tons	230	233	217	174	262
CPUE 2	Boats over 100 tons	—	4 316	4 222	5 472	—

[a] Data from Aomori Prefecture Fisheries Experimental Station
[b] Boats equipped with freezer

Table 24

Catch in weight per fishing day (CPUE 1) and catch in number per fishing day (CPUE 2) by jigging boats for *O. bartrami*[a]

	Year	Boats under 29 t	Boats of 30-99 t	Boats over 100 t
CPUE 1 (kg)[b]	1978	759	1 722	2 491
	1979	529	1 347	2 303
CPUE 2[c]	1978	1 420	3 330	4 980
	1979	1 140	2 500	5 820

	Year	Up to 9 t	10-20 t	20-30 t	30-40 t	40-50 t	50-60 t	60-70 t	70-80 t	80-90 t
CPUE 1 (kg)[d]	1978	860	618	828	1 452	1 463	1 480	1 733	1 514	1 169
	1979	293	617	726	967	1 211	867	1 019	1 187	1 054

	Year	90-100 t	100-200 t	200-300 t	300-400 t	Over 400 t
CPUE 1 (kg)[d]	1978	1 856	2 299	2 454	2 785	2 898
	1979	1 594	1 915	2 243	2 431	2 517

a/ Data from Hokkaido Reg. Fish. Res. Lab.

b/ Waters west of 170°E in July-October

c/ Estimated from Table 28

d/ Waters west of 180° in July-December

Table 25

Catch in weight (kg) per fishing day (CPUE) by waters by tonnage class of boats for *Ommastrephes bartrami*[a]

Tonnage class	Year	Up to 144°E		145°-149°E		150°-154°E		155°-159°E		160°-164°E		165°-169°E	
		N[b]	CPUE	N	CPUE	N	CPUE	N	CPUE	N	CPUE	N	CPUE
Boats under 29 t	1978	5	590	2	970	0	1 400	-	-	-	-	-	-
	1979	7	420	2	880	0	730	-	-	-	-	-	-
Boats of 30-99 t	1978	7	1 190	13	1 630	5	1 990	3	2 290	0	2 020	-	-
	1979	10	770	10	1 390	3	1 670	2	1 990	0	1 770	0	2 000
Boats over 100 t	1978	0	1 560	1	2 200	3	2 080	4	2 550	4	3 050	-	-
	1979	0	1 160	0	1 240	0	1 240	3	2 080	2	2 540	0	3 160

a/ Data from Hokkaido Reg. Fish. Res. Lab.

b/ N shows rank of numbers of fishing days: 0 = 10-99 days; 1 = 100-999 days; 2 = 1 000-1 999 days; 3 = 2 000-2 999 days; ----------; 13 = 12 000-12 999 days

Table 26

Number of 1 x 1 squares of latitude and longitude where the catch of *Ommastrephes bartrami* per fishing day per jigging boat (CPUE) was over 1.0 and 2.0 t[a]

		CPUE ≧1.0 ton[b]						CPUE ≧ 2.0 tons[b]					
		A[c]	B	C	D	E	Total	A	B	C	D	E	Total
August	1978	5	19	21	25	6	76	0	9	21	24	4	58
	1979	5	9	14	17	15	60	0	3	4	15	12	34
September	1978	10	22	24	14	16	86	1	9	17	9	14	50
	1979	2	16	17	16	9	60	0	3	3	13	6	25
October	1978	7	24	18	11	14	74	0	11	16	8	13	48
	1979	1	18	16	16	8	59	0	3	5	4	1	13

a/ Data from Hokkaido Reg. Fish. Res. Lab.

b/ Excluding the squares in which the number of fishing days were under 9

c/ A-E indicate the following waters: A: west of 144°E; B: 145°-164°E; C: 150° 150°-154°E; D: 155°-159°E; E: 160°-164°E

Table 27

Average body weights of *Ommastrephes bartrami* by waters (g)[a]

	Waters west of 149°E[b]		Waters west of 159°E[b]		Waters of 150°-165°E[c]	
	1978	1979	1978	1979	1978	1979
July	205	242	275	270	275	270
August	436	344	414	354	427	330
September	448	479	498	540	641	477
October	920	881	826	703	916	628

a/ Calculated from the data on the average dorsal mantle lengths by month and waters and the relationship between mantle length and body weight

b/ Data from Hokkaido Reg. Fish. Res. Lab.

c/ Data from Aomori Pre. Fish. Exp. St., based however on the assumption that body weights in July are the same as those of waters west of 159°E

Table 28

Estimates for fishing rate of *Todarodes pacificus* based on the results of tagging experiments[a]

Date released[b]	Number of squid released	Number of recaptured squid by days elapsed after release							Rate of recapture (%)	Fishing rate[c]				
										Method 1	Method 2		Method 3	
		0-30 days	31-60 days	61-90 days	91-120 days	121-150 days	?	Total		All fishing season	One month	Three months	One month	Three months
July 1952	1 200	195	14	5	0	2	5	221	0.184	0.475	0.161	0.409	0.202	0.305
August 1953	600	80	16	0	0	0	1	97	0.162	0.356	0.133	0.348	0.177	0.273
July 1954	608	109	27	2	0	0	0	138	0.227	0.473	0.184	0.457	0.240	0.373
July 1957	2 074	244	61	10	1	1	0	317	0.153	0.319	0.117	0.177	0.160	0.257
July 1958	1 926	197	21	2	0	0	0	220	0.114	0.286	0.102	0.312	0.131	0.201
July 1959	1 391	162	41	7	0	0	0	210	0.151	0.317	0.118	0.276	0.159	0.255
								Average	0.165	0.371	0.136	0.314	0.178	0.277

a/ Murata and Araya, 1970

b/ Released in the waters around Kojima Is. off southern Hokkaido

c/ Method 1: Tauchi, 1963; Method 2: Rounsefell and Everhart, 1956;
Method 3: Tanaka, 1967, 1968

Table 29

Estimates for fishing rates of *Todarodes pacificus*
based on the results of tagging experiments[a]

(1) Result of tagging experiment

St. No.	B	C	D	E	F	G	H	Total
Date released	30.6	13-20.7	23,29.7	29.8-1.9	15-20.9	22-23.9	22-23.10	31.5-23.10
No. of squid released	700	3,020	1,480	5,500	2,800	1,500	3,700	19,300
No.of squid recaptured	58	151	121	201	183	23	164	921
Elasped days 0-10	9	73	54	64	56	2	85	343
11-20	16	33	27	54	41	3	10	184
21-30	17	21	13	32	42	3	22	150
31-40	8	9	12	16	18	2	33	101
41-50	4	8	8	24	10	3	3	62
51-60	2	2	3	5	4	1	7	26
61-70	1	5	0	1	11	5	0	27
71-80	0	0	2	3	1	3	0	15
81-90	1	0	0	2	0	1	2	9
91-100	0	0	2	0	0	0	2	4
(2) Method of Beverton-Holt (Kato and Yamada, 1975)								
Coefficient of regression	3.016	4.053	3.884	4.371	4.323	0.984	3.850	5.879
Coefficient of total motality for 10 days	0.436	0.522	0.519	0.510	0.505	0.041	0.448	0.470
Rate of total motality for 10 days	0.353	0.407	0.405	0.400	0.396	0.040	0.361	0.375
Coefficient of fishing motality for 10 days	0.036	0.024	0.042	0.018	0.034	0.002	0.016	0.023
Fishing rate for 10 days	0.029	0.019	0.033	0.014	0.027	0.002	0.013	0.019
Coefficient of motality except fishing	0.400	0.497	0.477	0.492	0.470	0.039	0.433	0.447
Rate of motality except fishing	0.324	0.388	0.372	0.385	0.369	0.038	0.349	0.356
(3) Method of Tanaka (Tanaka, 1965)								
Mean of days elapsed after release	27.966	16.669	20.180	22.159	22.590	45.391	19.673	22.575
Coefficient of total motality for 10 days	0.358	0.600	0.496	0.451	0.443	0.220	0.508	0.443
Coefficient of fishing motality for 10 days	0.030	0.030	0.041	0.016	0.029	0.003	0.023	0.021
Coefficient of motality except fishing	0.327	0.570	0.455	0.435	0.414	0.217	0.486	0.422
Fishing rate	0.084	0.050	0.082	0.037	0.065	0.015	0.045	0.048

[a] Machinaka *et al.*, 1980

Table 30

Estimates for coefficient of fishing mortality (F) and coefficient of mortality except fishing (M) for *Todarodes pacificus* to the change of rate of mortality by tagging (α) and rate of recovery and report (β) (rate of total mortality = 0.443)a/

β α		0	5	10	15	20	25	30	35	40	45	50
100	F	0.021	0.022	0.024	0.025	0.027	0.028	0.030	0.033	0.035	0.039	0.043
	M	0.422	0.421	0.419	0.418	0.416	0.415	0.413	0.410	0.408	0.404	0.400
95		0.022	0.024	0.025	0.026	0.028	0.030	0.032	0.034	0.037	0.041	0.045
		0.421	0.419	0.418	0.417	0.415	0.413	0.411	0.409	0.406	0.402	0.398
90		0.024	0.025	0.026	0.028	0.030	0.031	0.034	0.036	0.039	0.043	0.047
		0.419	0.418	0.417	0.415	0.413	0.412	0.409	0.407	0.404	0.400	0.396
85		0.025	0.026	0.028	0.029	0.031	0.033	0.036	0.038	0.042	0.045	0.050
		0.418	0.417	0.415	0.414	0.412	0.410	0.407	0.405	0.401	0.398	0.393
80		0.027	0.028	0.030	0.031	0.033	0.035	0.038	0.041	0.044	0.048	0.053
		0.416	0.415	0.413	0.412	0.410	0.408	0.405	0.402	0.399	0.395	0.390
75		0.023	0.030	0.031	0.033	0.035	0.038	0.040	0.044	0.047	0.052	0.057
		0.415	0.413	0.412	0.410	0.408	0.405	0.403	0.399	0.396	0.391	0.386
70		0.030	0.032	0.034	0.036	0.038	0.040	0.043	0.047	0.051	0.055	0.061
		0.413	0.411	0.409	0.407	0.405	0.403	0.400	0.396	0.392	0.388	0.382
65		0.033	0.034	0.036	0.038	0.041	0.044	0.047	0.050	0.054	0.059	0.065
		0.410	0.409	0.407	0.405	0.402	0.399	0.396	0.393	0.389	0.384	0.378
60		0.035	0.037	0.039	0.042	0.044	0.047	0.051	0.054	0.059	0.064	0.071
		0.408	0.406	0.404	0.401	0.399	0.396	0.392	0.389	0.384	0.379	0.372
55		0.039	0.041	0.043	0.045	0.048	0.025	0.055	0.059	0.064	0.070	0.077
		0.404	0.402	0.400	0.398	0.395	0.391	0.388	0.384	0.379	0.373	0.366
50		0.043	0.045	0.047	0.050	0.053	0.057	0.061	0.065	0.071	0.077	0.085
		0.400	0.398	0.396	0.393	0.390	0.386	0.382	0.378	0.372	0.366	0.358

a/ Machinaka *et al.*, 1980

Table 31

Fishing rate (E) and population abundance (P) of *Todarodes pacificus* in waters of northern Japana/

Year	E	P (10 t)	Year	E	P (10 t)
1952	0.390	1 352	1962	0.496	951
1953	0.416	815	1963	0.496	963
1954	0.381	918	1964	0.482	366
1955	0.379	899	1965	0.397	829
1956	0.396	623	1966	0.447	705
1957	0.418	716	1967	0.477	814
1958	0.403	756	1968	0.499	1 089
1959	0.448	940	1969	0.493	738
1960	0.405	982	1970	0.500	545
1961	0.454	701	1971	0.494	460

a/ Araya, 1974

Table 32

Biomass analysis for the winter group of *Todarodes pacificus*[a]

Month	W[b]	S[b] = 0.4		S = 0.5		S = 0.6		S = 0.7		S = 0.8		S = 0.9	
		N[b]	NW	N	NW	N	NW	N	NW	N	NW	N	NW
Mar.	2.5	10 000	25 000	10 000	25 000	10 000	25 000	10 000	25 000	10 000	25 000	10 000	25 000
Apr.	15	4 000	60 000	5 000	75 000	6 000	90 000	7 000	105 000	8 000	120 000	9 000	135 000
May	39	1 600	62 400	2 500	97 500	3 600	140 400	4 900	191 100	6 400	249 600	8 100	315 900
June	72	640	46 080	1 250	90 000	2 160	155 520	3 430	246 960	5 120	368 640	7 290	524 880
July	109	256	27 904	625	68 125	1 296	141 264	2 401	261 709	4 096	446 464	6 561	715 149
Aug.	148	102	15 096	312	46 176	778	115 144	1 681	248 788	3 277	484 996	5 905	873 940
Sep.	187	40.8	7 630	156	29 172	467	87 329	1 176	219 912	2 621	490 127	5 314	993 718
Oct.	225	16.4	3 690	78	17 550	280	63 000	824	185 400	2 097	471 825	4 783	1 076 175
Nov.	259	6.6	1 706	39	10 101	168	43 512	576	149 184	1 678	434 602	4 305	1 114 995
Dec.	291	2.6	757	19.5	5 675	101	29 391	404	117 564	1 342	390 522	3 874	1 127 334
Jan.	318	1.0	318	9.8	3 116	60	19 080	282	89 676	1 073	341 214	3 487	1 108 866
Feb.	342	0.4	137	4.9	1 676	36	12 312	198	67 716	859	293 778	3 138	1 073 196

[a] Doi and Kawakami, 1979

[b] W: body weight in g; S: survival rate for a month after young stage; N: number of squid

Table 33

Estimates for reproduction potential and fishing productivity for the winter group of *Todarodes pacificus*[a]

(M[b] = 0.4308) Month[c]	W[b]	F[b] = 0, M+F = 0.4308 S[b] = 0.65, E[b] = 0			F = 0.1, M+F = 0.5308 S = 0.5881, E = 0.0776			F = 0.2, M+F = 0.6308 S = 0.5322, E = 0.1483		
		N[b]	NW	ENW	N	NW	ENW	N	NW	ENW
Mar.	2.5	10 000	25 000		10 000	25 000		10 000	25 000	
Apr.	15	6 500	97 500		6 500	97 500		6 500	97 500	
May	39	4 225	164 775		4 225	164 775		4 225	164 775	
June	72	2 746	197 712	0	2 746	197 712	15 342	2 746	197 712	29 321
July	109	1 785	194 565	0	1 615	176 035	13 660	1 462	159 358	23 632
Aug.	148	1 160	171 680	0	950	140 600	10 910	778	115 144	17 075
Sep.	187	754	140 998	0	559	104 533	8 111	414	77 418	11 481
Oct.	225	490	110 250	0	329	74 025	5 744	220	49 500	7 340
Nov.	259	319	82 621	0	193	49 987	3 879	117	30 303	4 493
Dec.	291	207	60 237	0	114	33 174	2 574	62	18 402	2 675
Jan.	318	135	42 930	0	66.8	21 242	1 648	33.2	10 558	1 565
Feb.	342	87	29 754	0	39.3	13 441	1 043	17.7	6 053	897
(1) and (2)[d]		111		0	53		62 911	25.5		98 479
(3)			134.2			122.6			113.5	
(4)		100			48			23		
(5)			837 422			629 110			492 395	
(6)			100			75			59	

(M[b] = 0.4308) Month[c]	W[b]	F = 0.3, M+F = 0.7308 S = 0.4815, E = 0.2128			F = 0.4, M+F = 0.8308 S = 0.4357, E = 0.2717			F = 0.5, M+F = 0.9308 S = 0.3942, E = 0.3254		
		N	NW	ENW	N	NW	ENW	N	NW	ENW
Mar.	2.5	10 000	25 000		10 000	25 000		10 000	25 000	
Apr.	15	6 500	97 500		6 500	97 500		6 500	97 500	
May	39	4 225	164 775		4 225	164 775		4 225	164 775	
June	72	2 746	197 712	42 073	2 746	197 712	53 718	2 746	197 712	64 335
July	109	1 322	144 098	30 664	1 197	130 473	35 449	1 083	118 047	38 412
Aug.	148	637	94 276	20 062	521	77 108	20 950	427	63 196	20 564
Sep.	187	307	57 409	12 216	227	42 449	11 533	168	31 416	10 222
Oct.	225	148	33 300	7 086	99	22 275	6 052	66.3	14 917	4 854
Nov.	259	71	18 389	3 913	43.1	11 163	3 033	26.1	6 760	2 199
Dec.	291	34.2	9 952	2 117	18.8	5 471	1 486	10.3	2 997	975
Jan.	318	16.5	5 247	1 116	8.2	2 608	708	4.1	1 304	424
Feb.	342	7.9	2 702	575	3.6	1 231	334	1.6	547	178
(1) and (2)[d]		12.2		119 822	5.9		133 263	2.9		142 163
(3)			106.5			100.8			96.4	
(4)		11			5			3		
(5)			399 407			333 158			284 326	
(6)			48			40			33	

[a] Doi and Kawakami, 1979

[b] M: coefficient of natural mortality; F: coefficient of fishing mortality; E: fishing rate, S, W and N: see Table 32

[c] Fishing season: June-February

[d] (1) number of adult squid; (2) total catch; (3) mean of body weight (g) in fishing season; (4) rate of decrease of reproduction potential (%); (5) fishing productivity; (6) rate of decrease of fishing productivity (%)

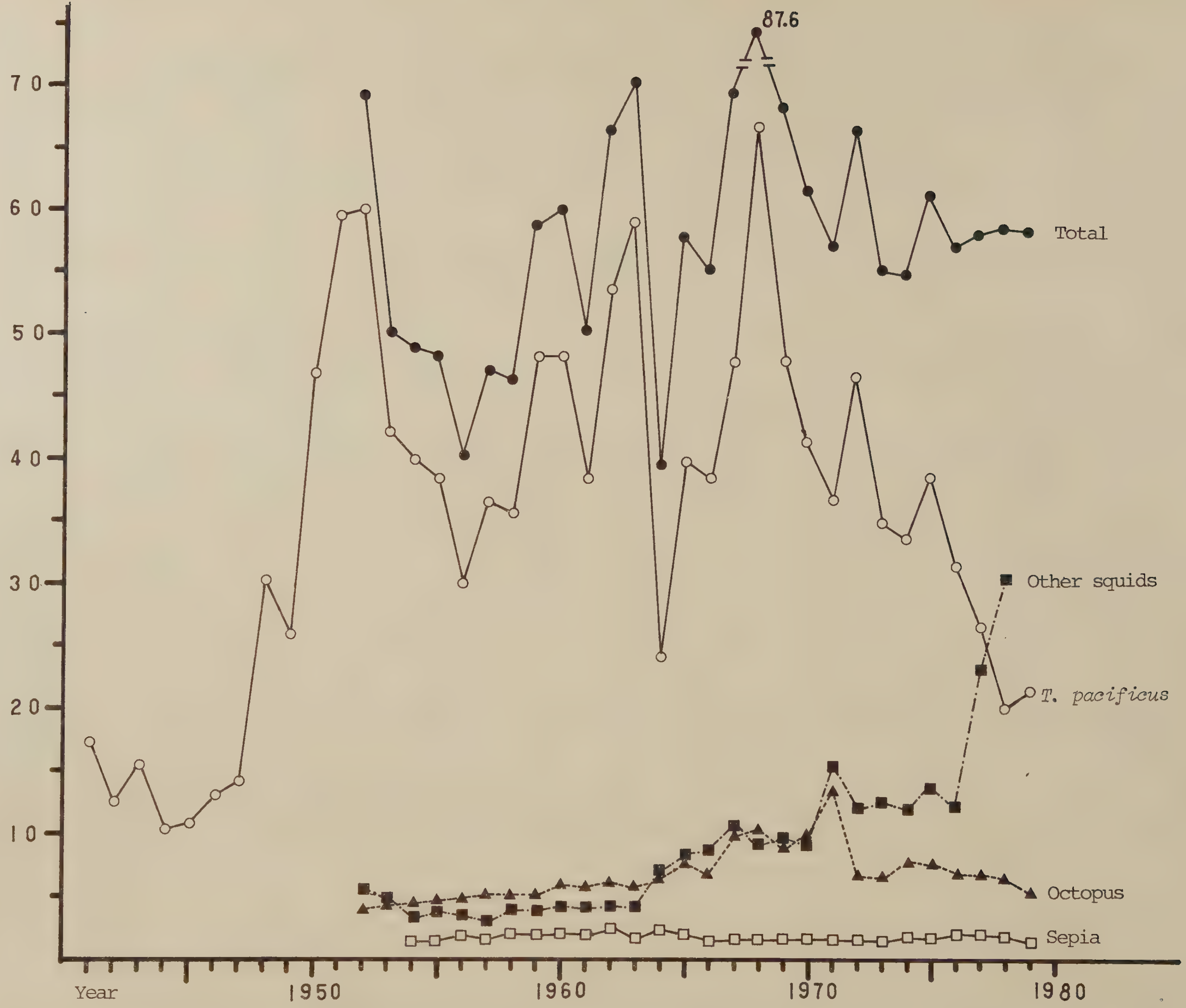


Fig. 1 Annual catches of squids and octopuses in Japan (in 10 000 t)

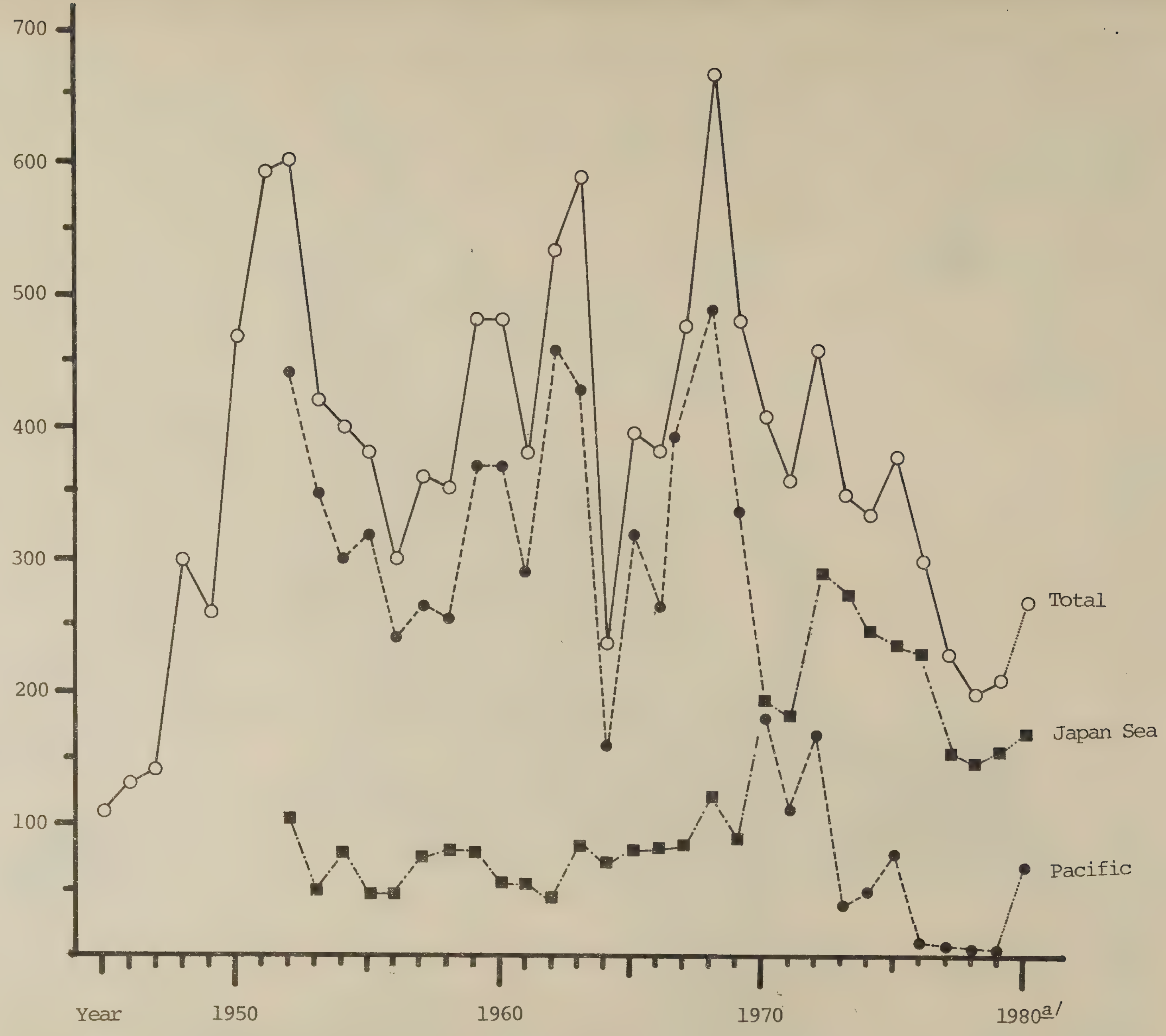


Fig. 2 Annual catches of *Todarodes pacificus* in the Pacific and the Japan Sea (in 10 000 t)

a/ Preliminary

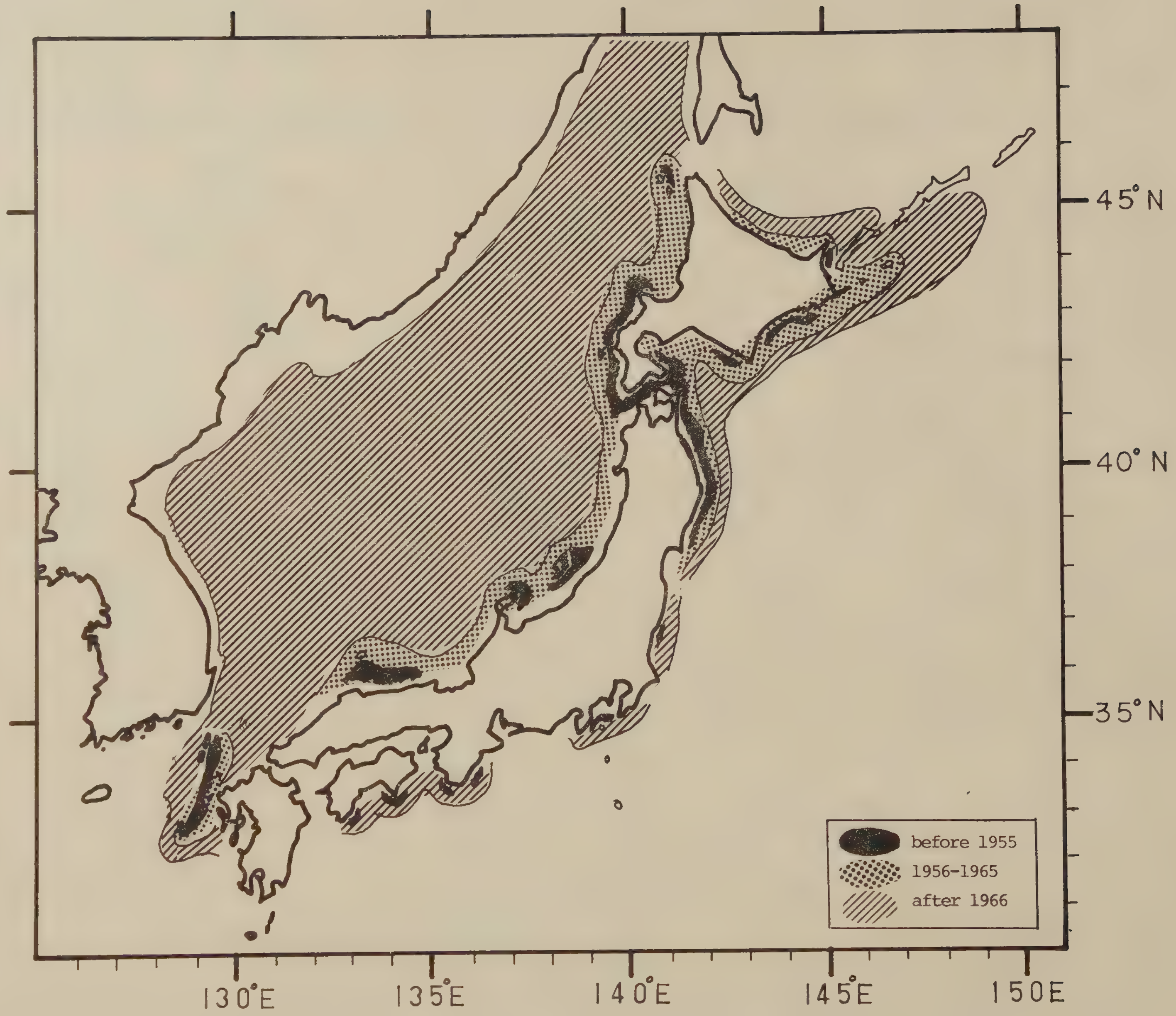

45°N
40°N
35°N
130°E
135°E
140°E
145°E
150E
before 1955
1956-1965
after 1966

Fig. 3 History of the expansion of *Todarodes pacificus* fishing grounds

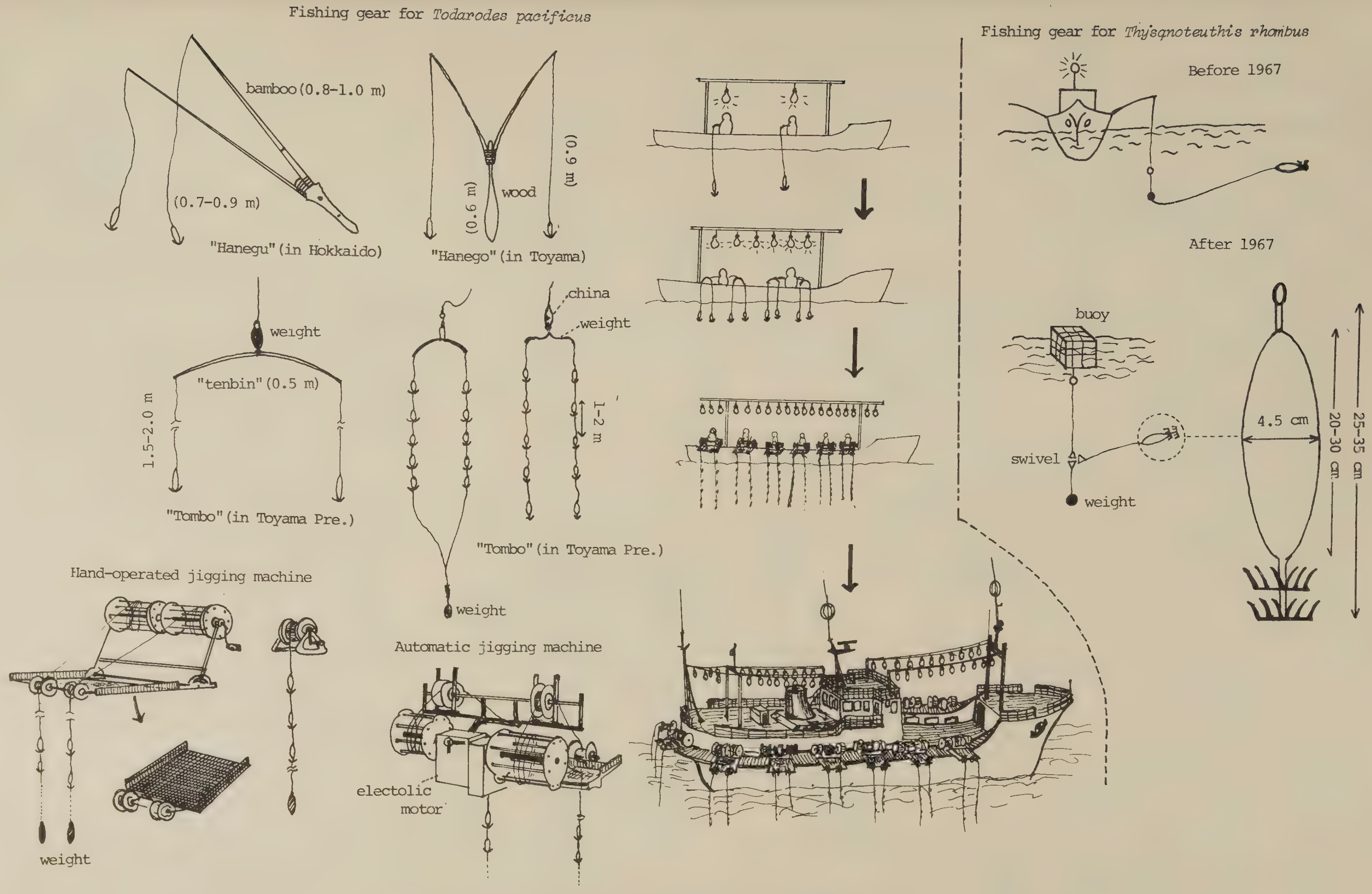

Fishing gear for *Todarodes pacificus*
bamboo (0.8-1.0 m)
(0.7-0.9 m)
"Hanegu" (in Hokkaido)
wood
(0.6 m)
(0.9 m)
"Hanego" (in Toyama)
weight
"tenbin" (0.5 m)
1.5-2.0 m
"Tombo" (in Toyama Pre.)
china
weight
1-2 m
"Tombo" (in Toyama Pre.)
weight
Hand-operated jigging machine
weight
Automatic jigging machine
electolic motor
Fishing gear for *Thysqnoteuthis rhombus*
Before 1967
After 1967
buoy
swivel
weight
4.5 cm
20-30 cm
25-35 cm

Fig. 4-1 Fishing gears for squid (FAO, 1976; Nazumi, 1975)

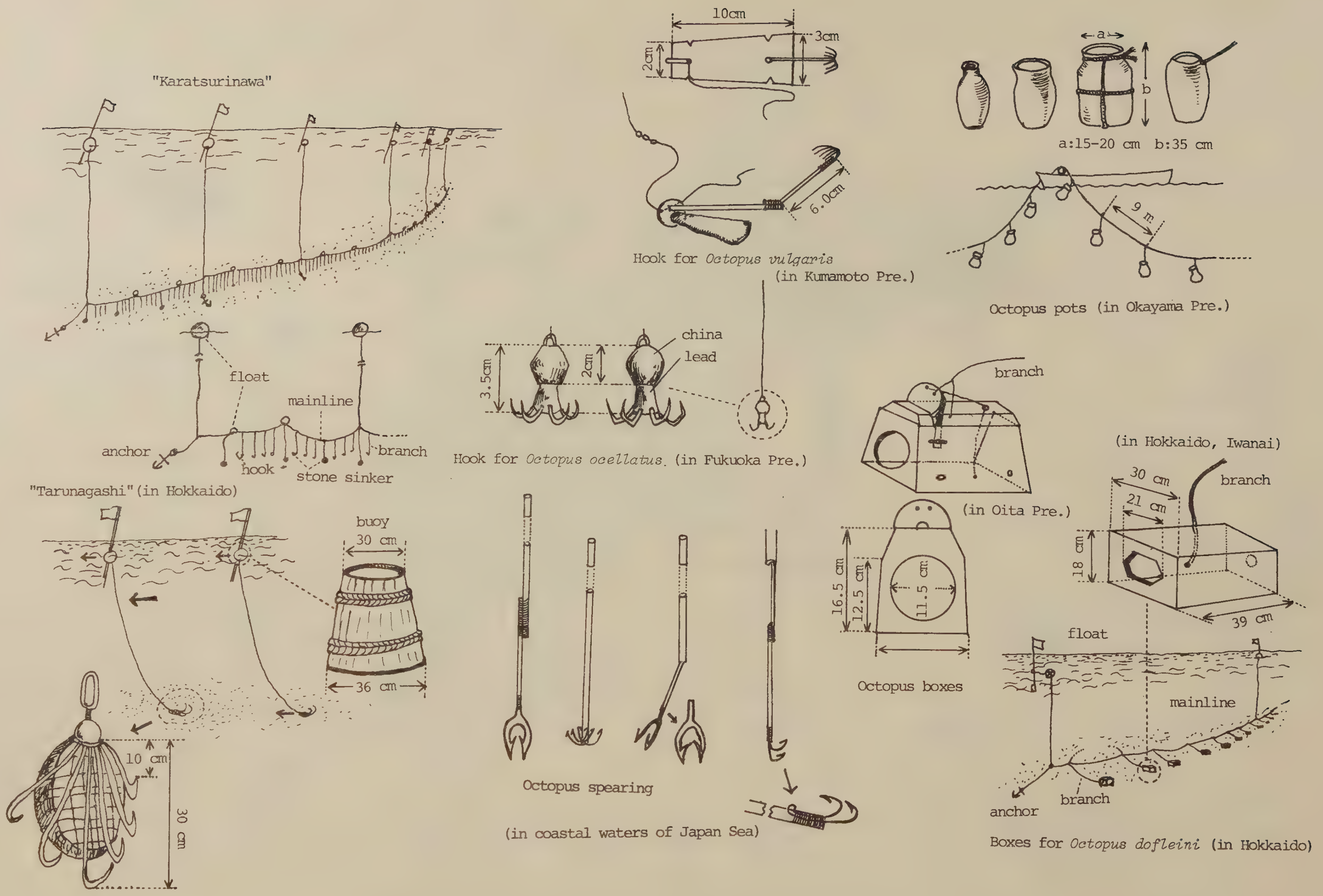

"Karatsurinawa"
10cm
3cm
2cm
6.0cm
Hook for *Octopus vulgaris*
(in Kumamoto Pre.)
a
b
a:15-20 cm b:35 cm
9 m
Octopus pots (in Okayama Pre.)
float
mainline
anchor
hook
stone sinker
branch
"Tarunagashi"(in Hokkaido)
3.5cm
2cm
china
lead
Hook for *Octopus ocellatus.* (in Fukuoka Pre.)
branch
(in Oita Pre.)
16.5 cm
12.5 cm
11.5 cm
Octopus boxes
(in Hokkaido, Iwanai)
30 cm
21 cm
18 cm
39 cm
branch
buoy
30 cm
36 cm
10 cm
30 cm
Octopus spearing
(in coastal waters of Japan Sea)
float
mainline
anchor
branch
Boxes for *Octopus dofleini* (in Hokkaido)

Fig. 4-2 Fishing gears for octopuses (FAO, 1976)

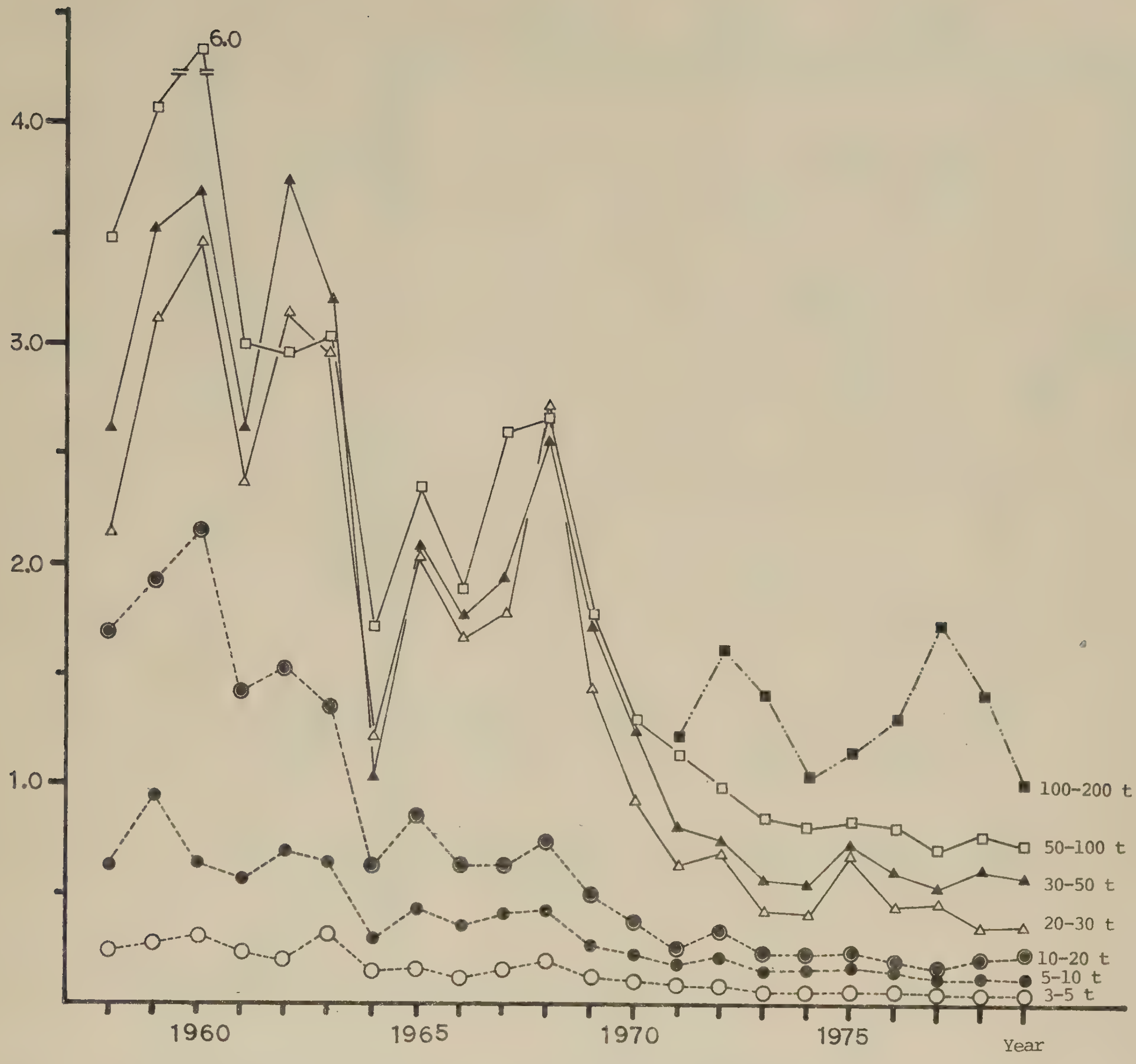


Fig. 5 Catch-per-fishing day, by size of boat, in squids angling fisheries (t)

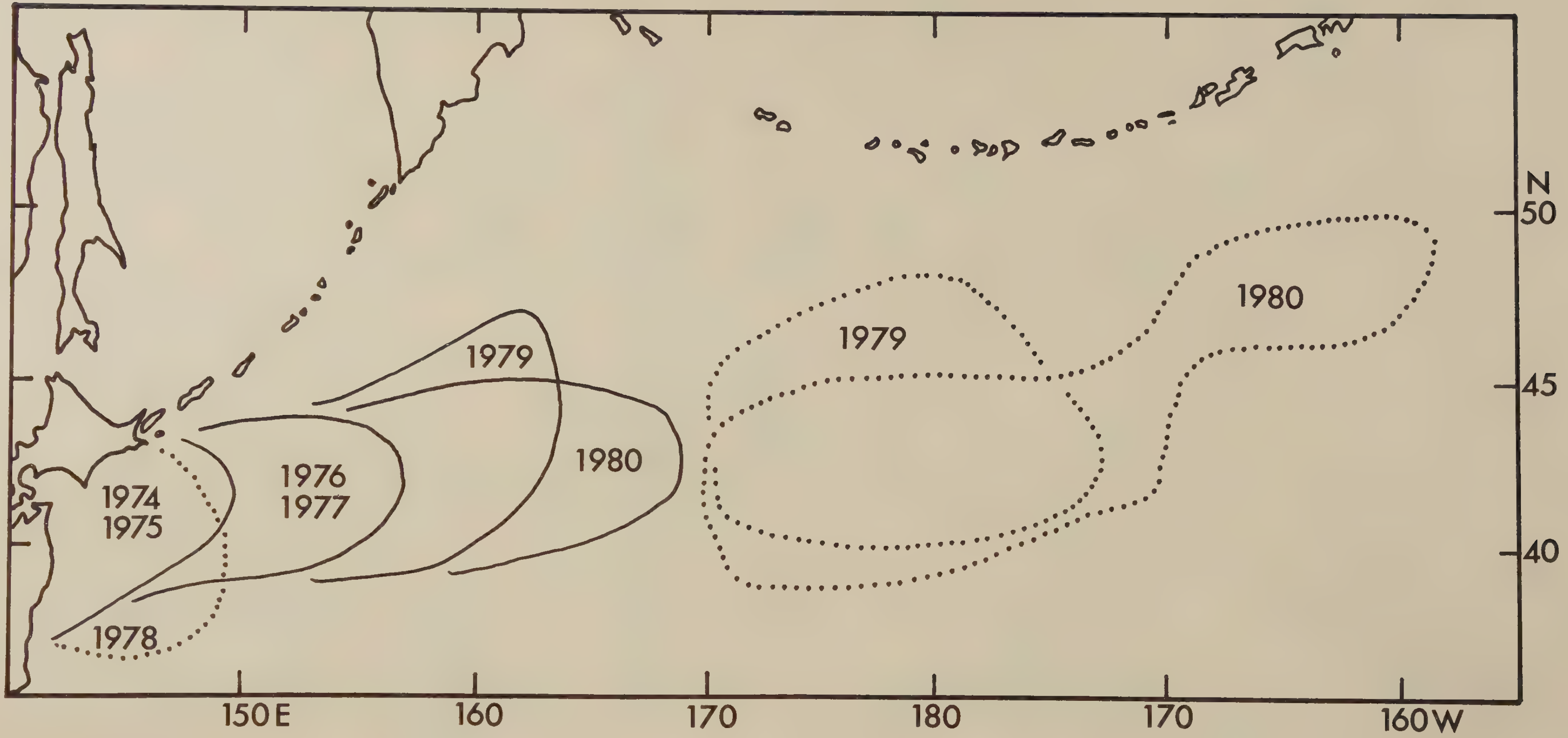

N
50
45
40
150E
160
170
180
170
160W
1974
1975
1976
1977
1978
1979
1980
1979
1980

Fig. 6 Periodic changes of annual fishing grounds for *Ommastrephes bartrami*

○ Jigging fishery ◌ Drift gillnets fishery

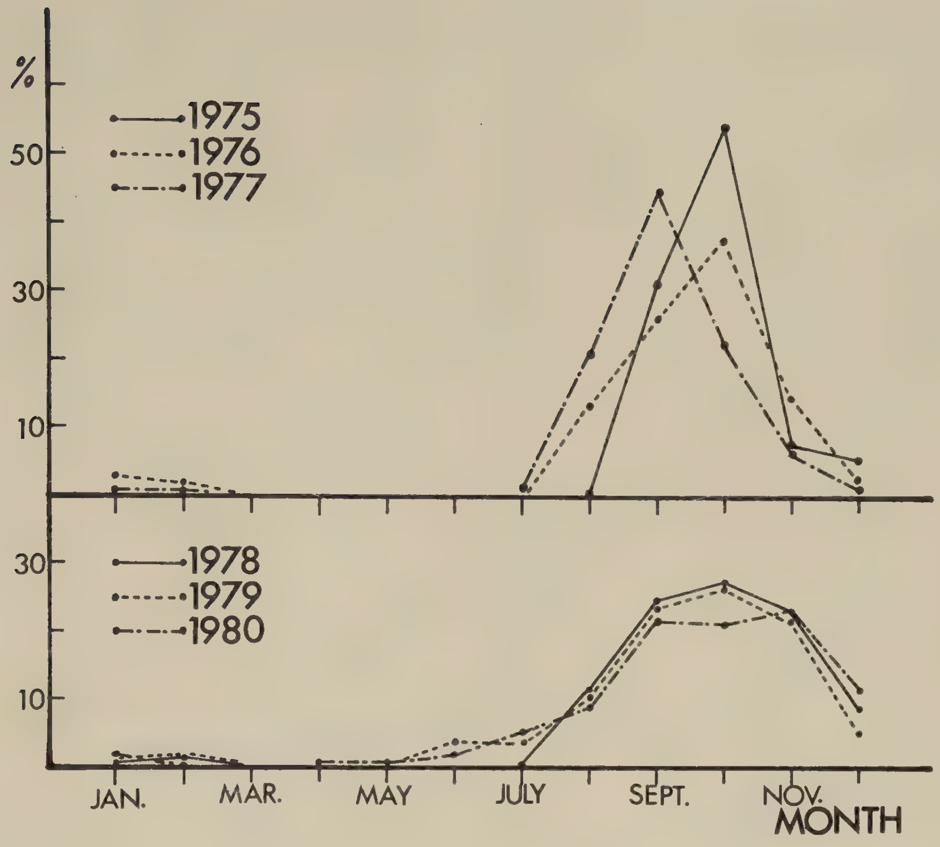


Fig. 7 Monthly catch of *Ommastrephes bartrami* in 1975-80 (%) 1975-77: by jigging; 1978-80: by jigging and by drift gillnets

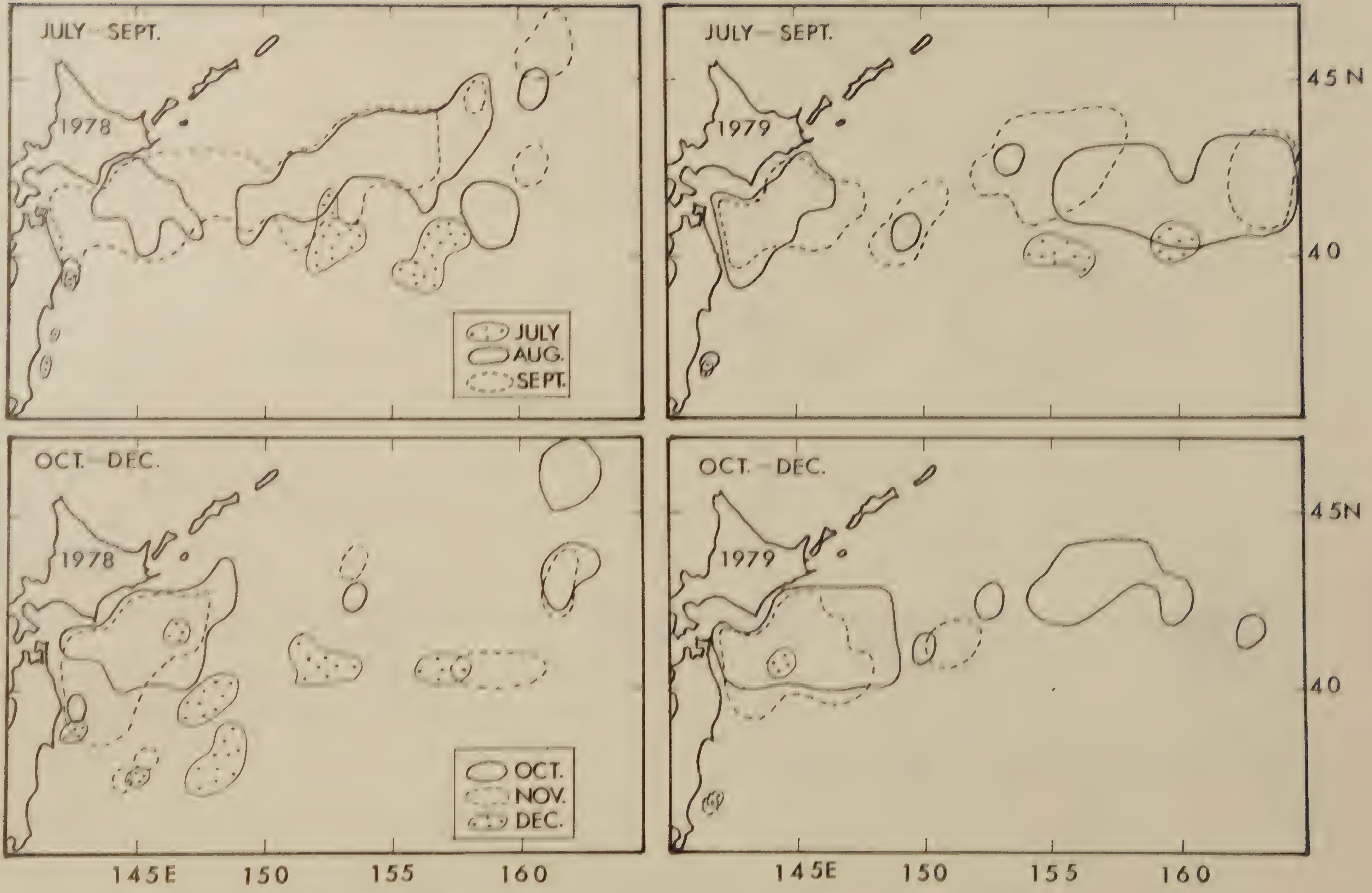
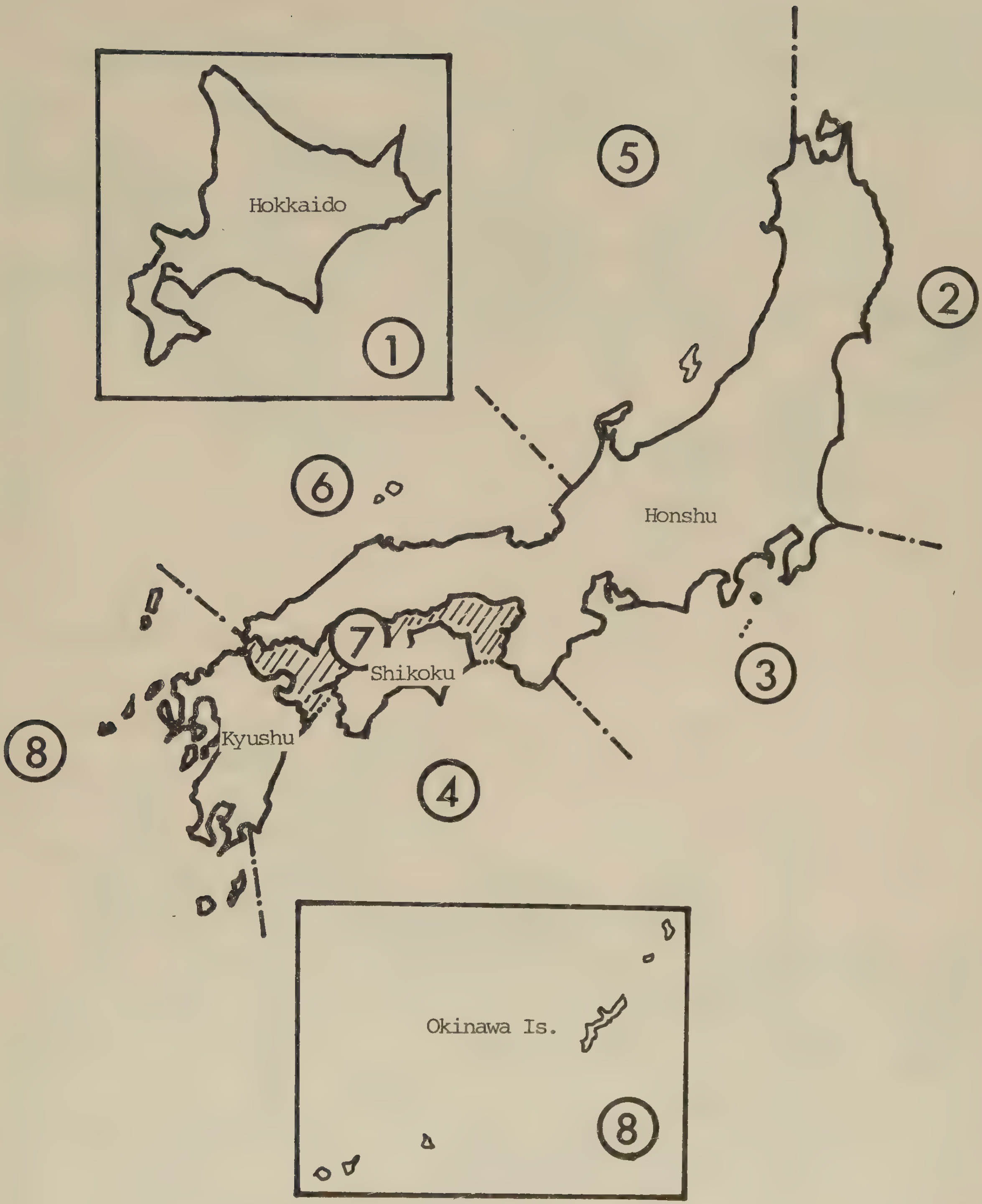

JULY—SEPT.
1978
JULY
AUG.
SEPT.
JULY—SEPT.
1979
45 N
40
OCT.—DEC.
1978
OCT.
NOV.
DEC.
OCT.—DEC.
1979
45N
40
145E
150
155
160
145E
150
155
160

Fig. 8 Monthly change of fishing grounds by jigging for *Ommastrephes bartrami* in 1978 and 1979


Hokkaido
①
⑤
②
⑥
Honshu
⑦
Shikoku
③
⑧
Kyushu
④
Okinawa Is.
⑧

1 : Hokkaido
2 : Northern Pacific Ocean
3 : Middle Pacific Ocean
4 : Southern Pacific Ocean
5 : Northern Japan Sea
6 : Western Japan Sea
7 : Seto Inland Sea
8 : East China Sea

Fig. 9 Subareas for Japanese fishery statistics (Statistics and Information Department, Ministry of Agriculture, Forestry and Fisheries)

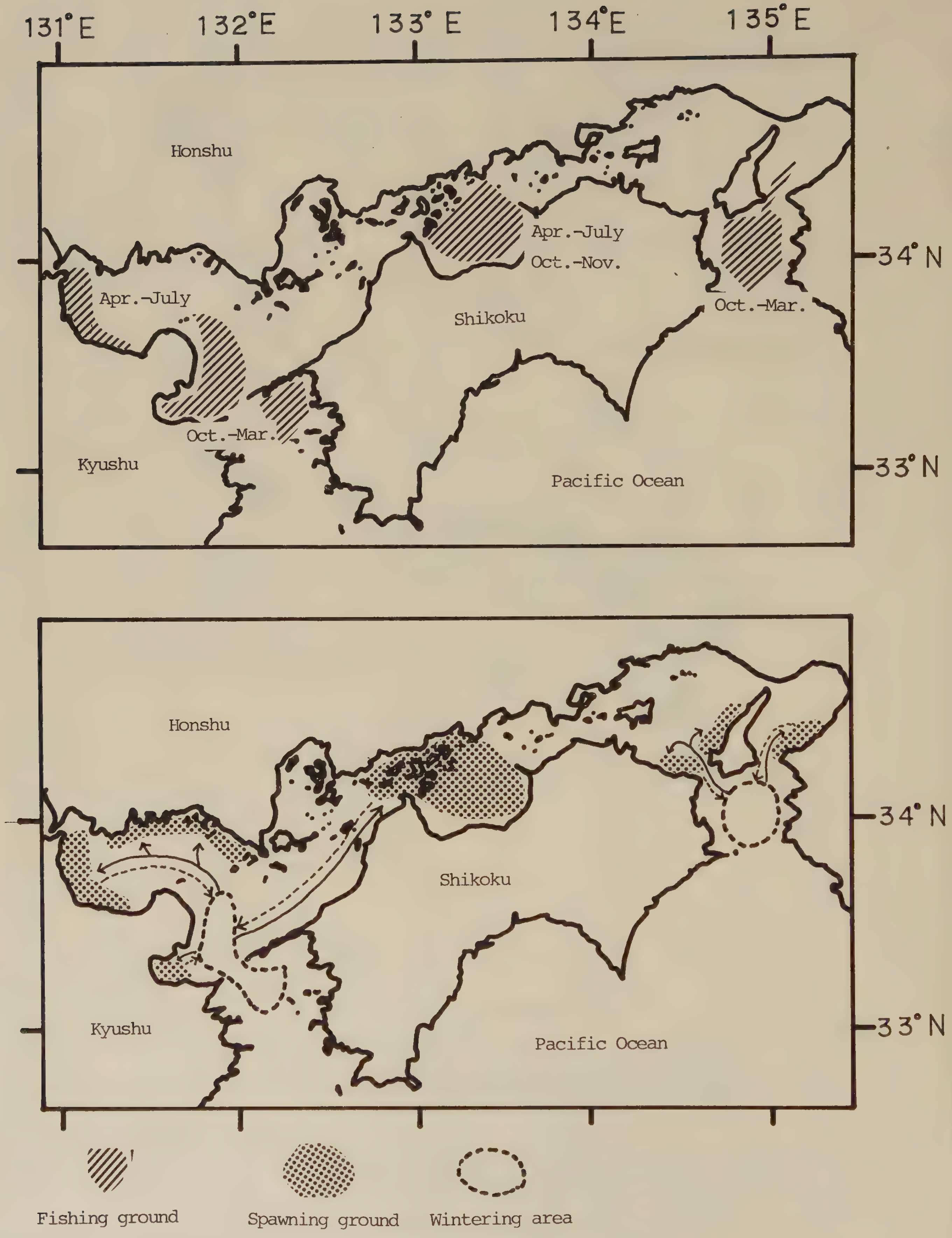

131°E
132°E
133° E
134°E
135°E
34° N
33° N
Honshu
Apr.-July
Oct.-Nov.
Apr.-July
Oct.-Mar.
Oct.-Mar.
Shikoku
Kyushu
Pacific Ocean
Honshu
Shikoku
Kyushu
Pacific Ocean
34° N
33° N
Fishing ground
Spawning ground
Wintering area

Fig. 10 Fishing season and grounds, spawning grounds and wintering area of *Sepiella japonica* in the Seto Inland Sea

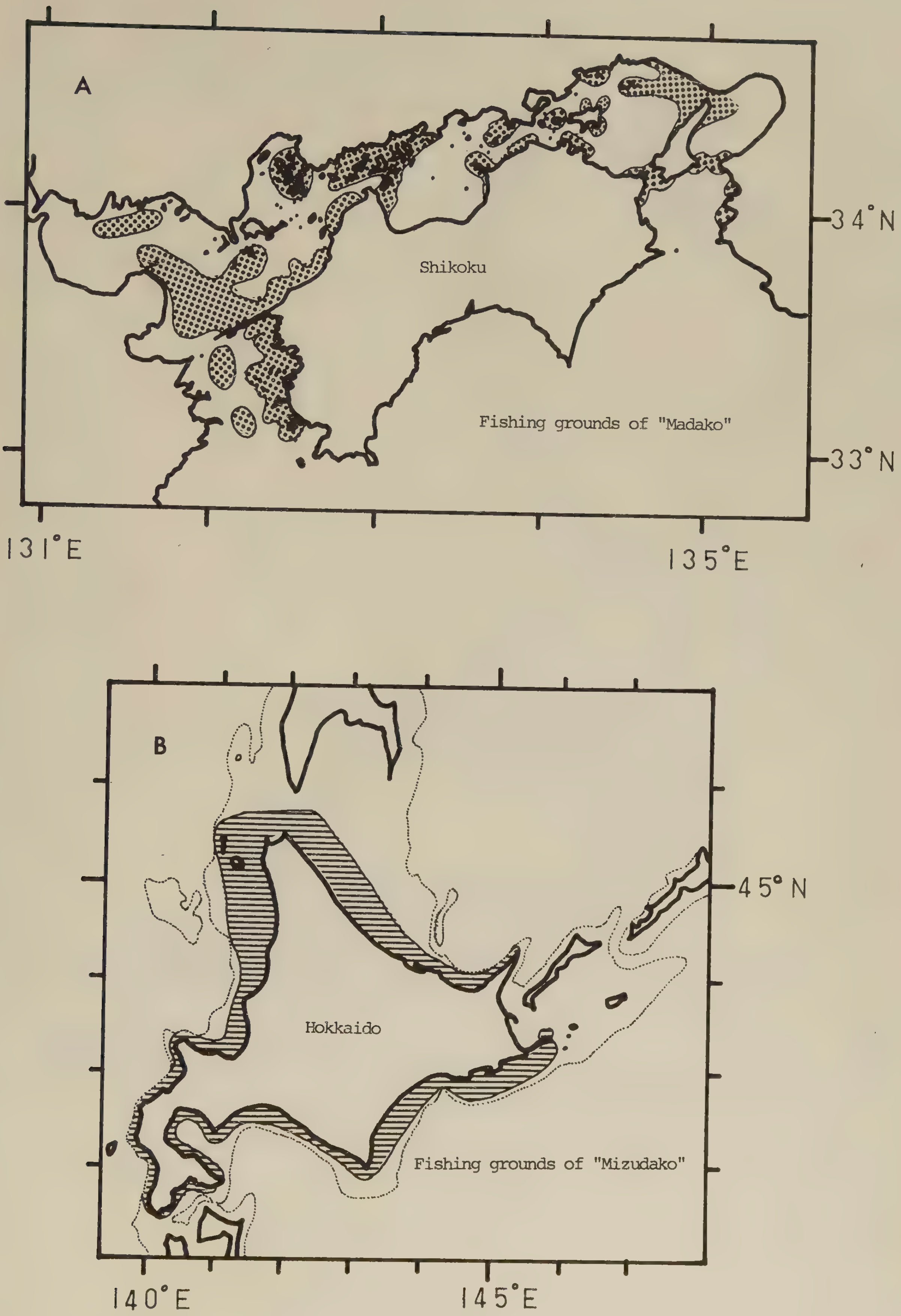

A
Shikoku
Fishing grounds of "Madako"
34°N
33°N
131°E
135°E
B
Hokkaido
Fishing grounds of "Mizudako"
45°N
140°E
145°E

Fig. 11 Fishing grounds of *Octopus vulgaris* ("Madako", upper panel) and *Octopus dofleini* ("Mizudako", lower panel)

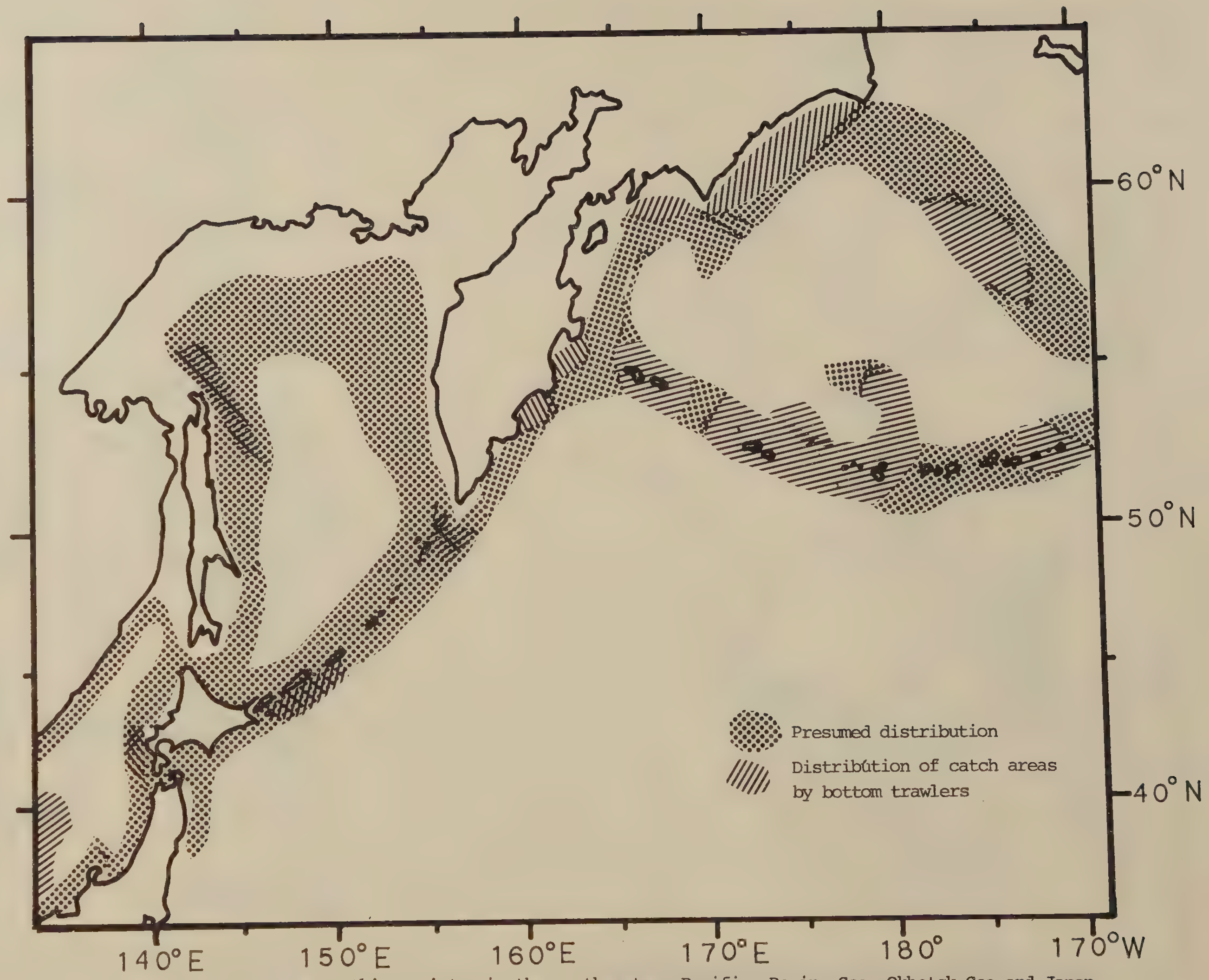

60°N
50°N
40°N
140°E
150°E
160°E
170°E
180°
170°W
Presumed distribution
Distribution of catch areas by bottom trawlers

Fig. 12 Distribution of *Berryteuthis magister* in the northwestern Pacific, Bering Sea, Okhotsk Sea and Japan Sea, 1969-71 and 1975 (Naito *et al.*, 1977)

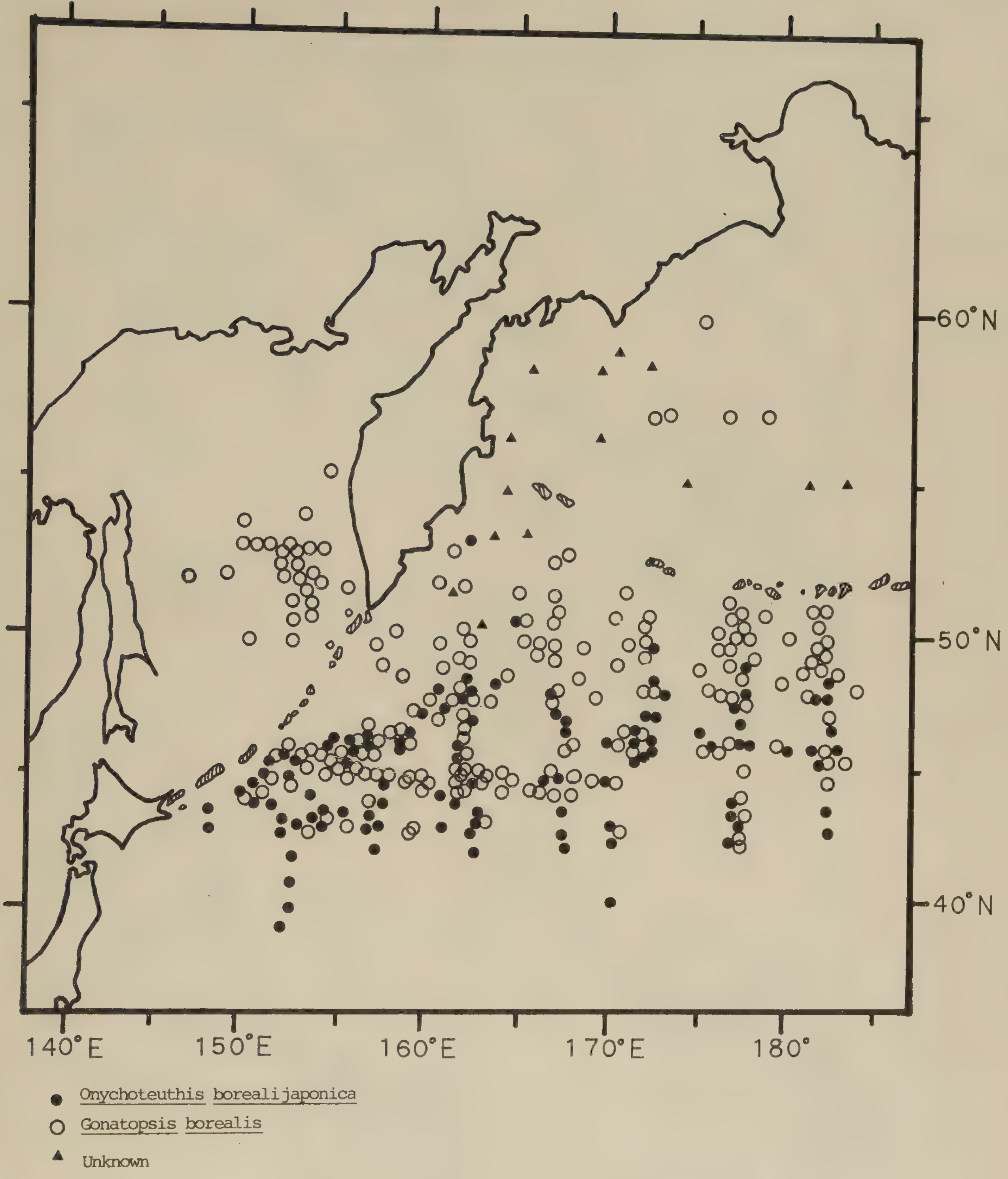

60°N
50°N
40°N
140°E
150°E
160°E
170°E
180°
● Onychoteuthis borealijaponica
○ Gonatopsis borealis
▲ Unknown

Fig. 13 Distribution of oceanic squids in the northwestern Pacific, Okhotsk Sea and Bering Sea from spring to summer in 1976 (Naito *et al.*, 1977)

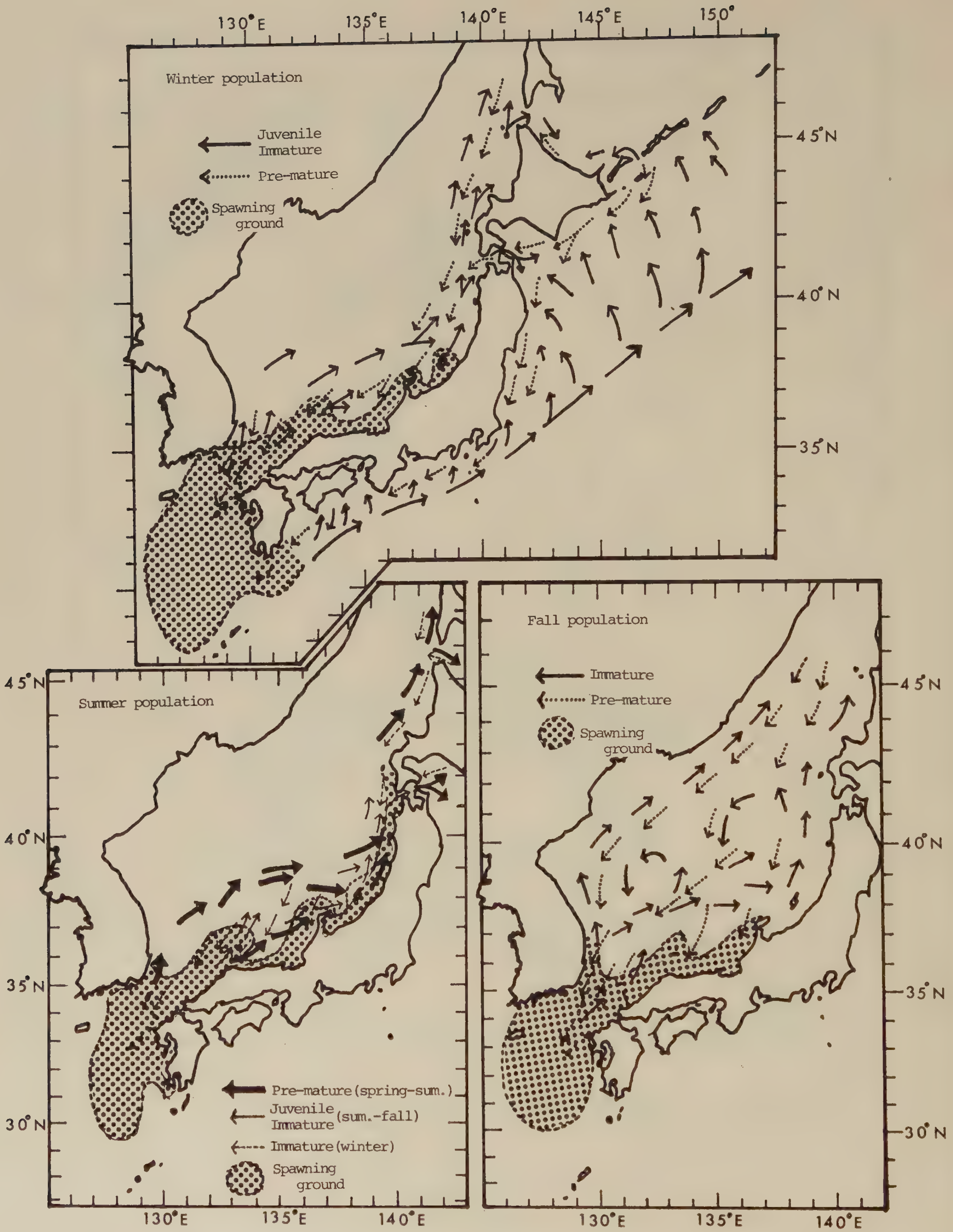

130°E
135°E
140°E
145°E
150°
45°N
40°N
35°N
Winter population
Juvenile
Immature
Pre-mature
Spawning ground
Summer population
45°N
40°N
35°N
30°N
Pre-mature (spring-sum.)
Juvenile
Immature
(sum.-fall)
Immature (winter)
Spawning ground
130°E
135°E
140°E
Fall population
Immature
Pre-mature
Spawning ground
45°N
40°N
35°N
30°N
130°E
135°E
140°E

Fig. 14 Schematic diagram of migration routes and spawning grounds of *Todarodes pacificus* in the Japanese coastal waters

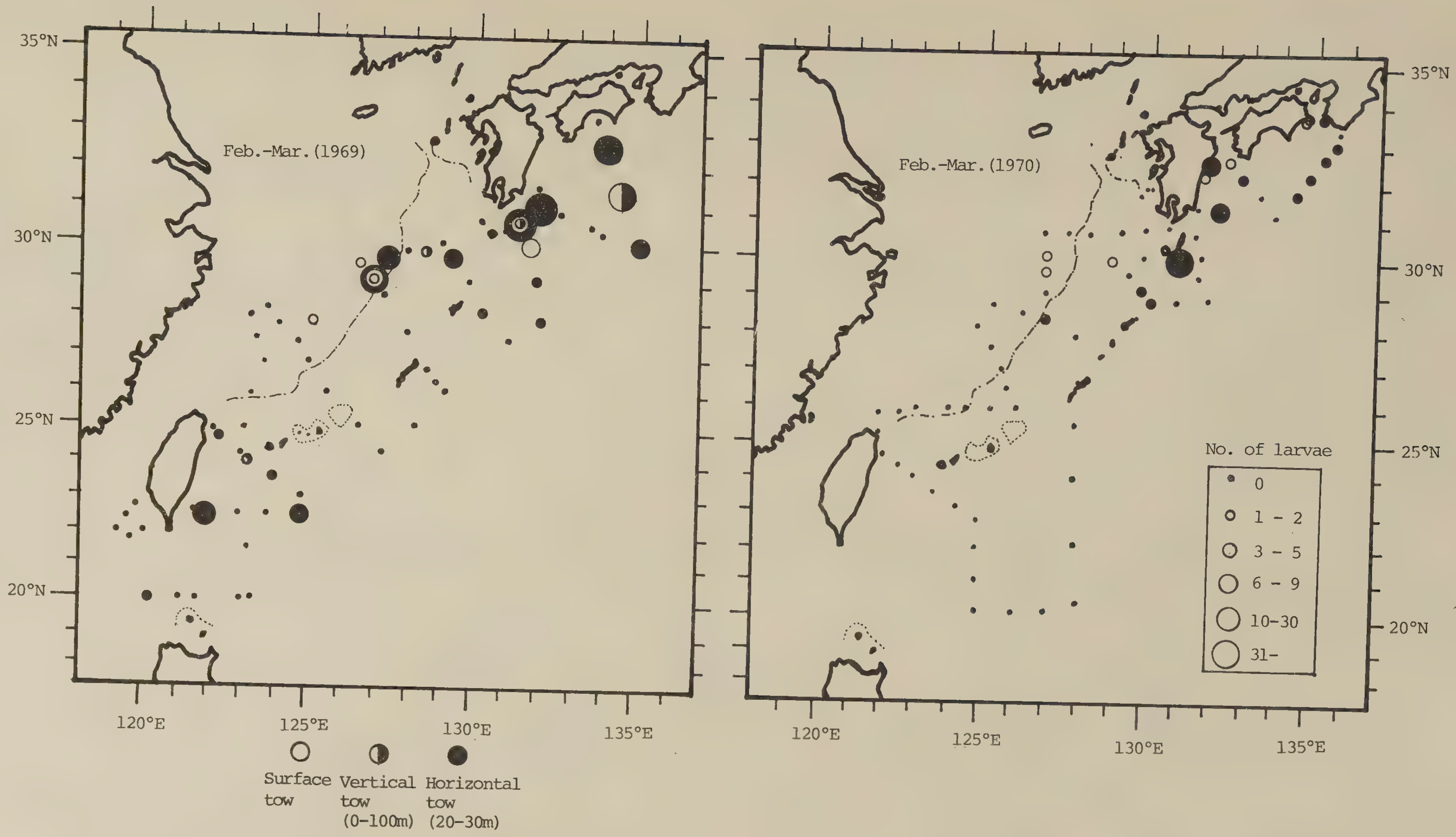

Feb.-Mar.(1969)
Feb.-Mar.(1970)
35°N
30°N
25°N
20°N
120°E
125°E
130°E
135°E
Surface tow
Vertical tow (0-100m)
Horizontal tow (20-30m)
No. of larvae
0
1 - 2
3 - 5
6 - 9
10-30
31-

Fig. 15 Distribution of *Todarodes pacificus* larvae bred in winter (based on Tech. Con. Min. Are. For. Fish., 1972)

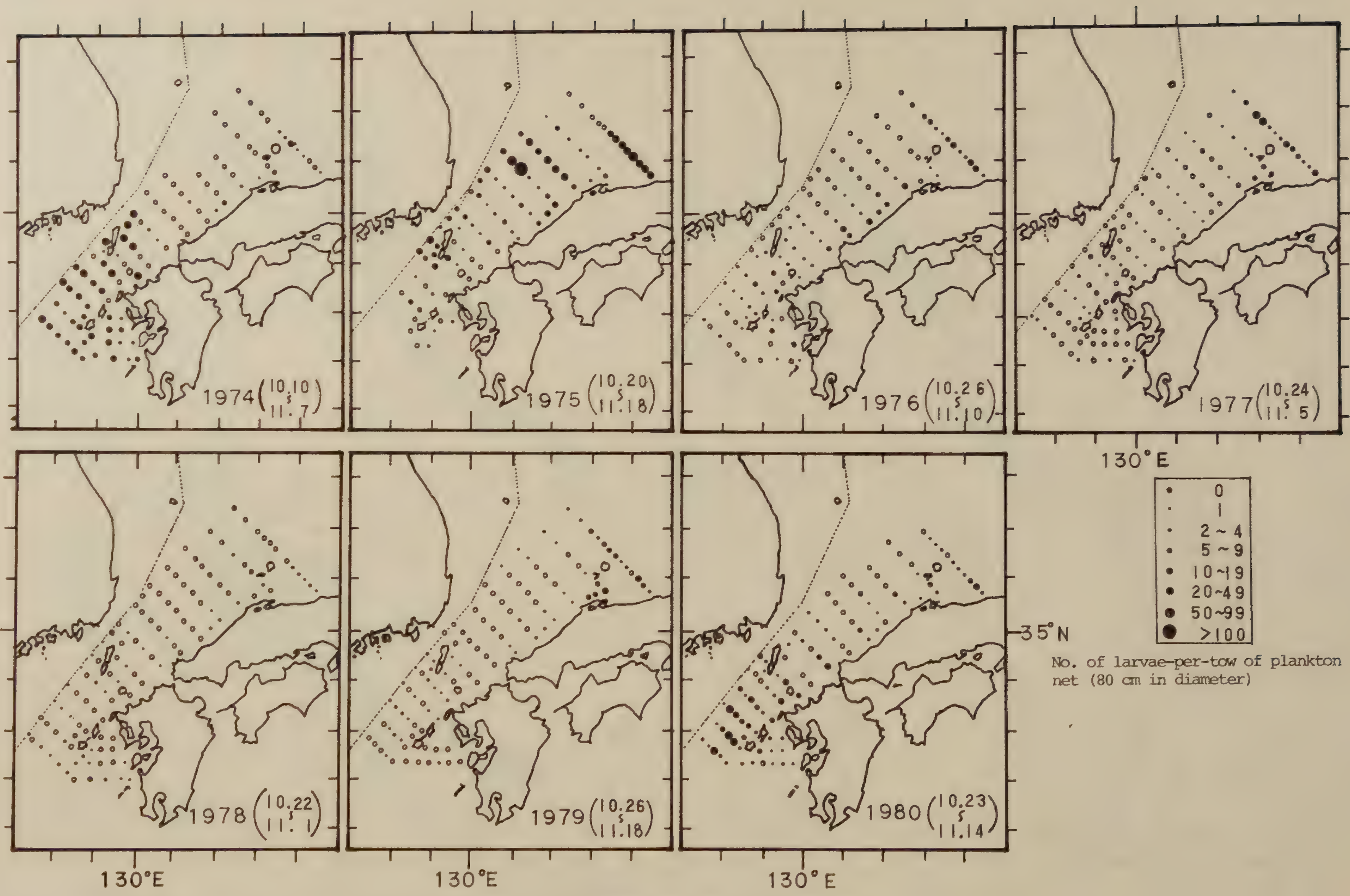

1974 (10.10 ~ 11.7)
1975 (10.20 ~ 11.18)
1976 (10.26 ~ 11.10)
1977 (10.24 ~ 11.5)
1978 (10.22 ~ 11.1)
1979 (10.26 ~ 11.18)
1980 (10.23 ~ 11.14)
35°N
130°E
0
1
2 ~ 4
5 ~ 9
10~19
20~49
50~99
>100
No. of larvae-per-tow of plankton net (80 cm in diameter)

Fig. 16 Distribution of *Todarodes pacificus* larvae bred in fall (Japan Sea Reg. Fish. Res. Lab.)

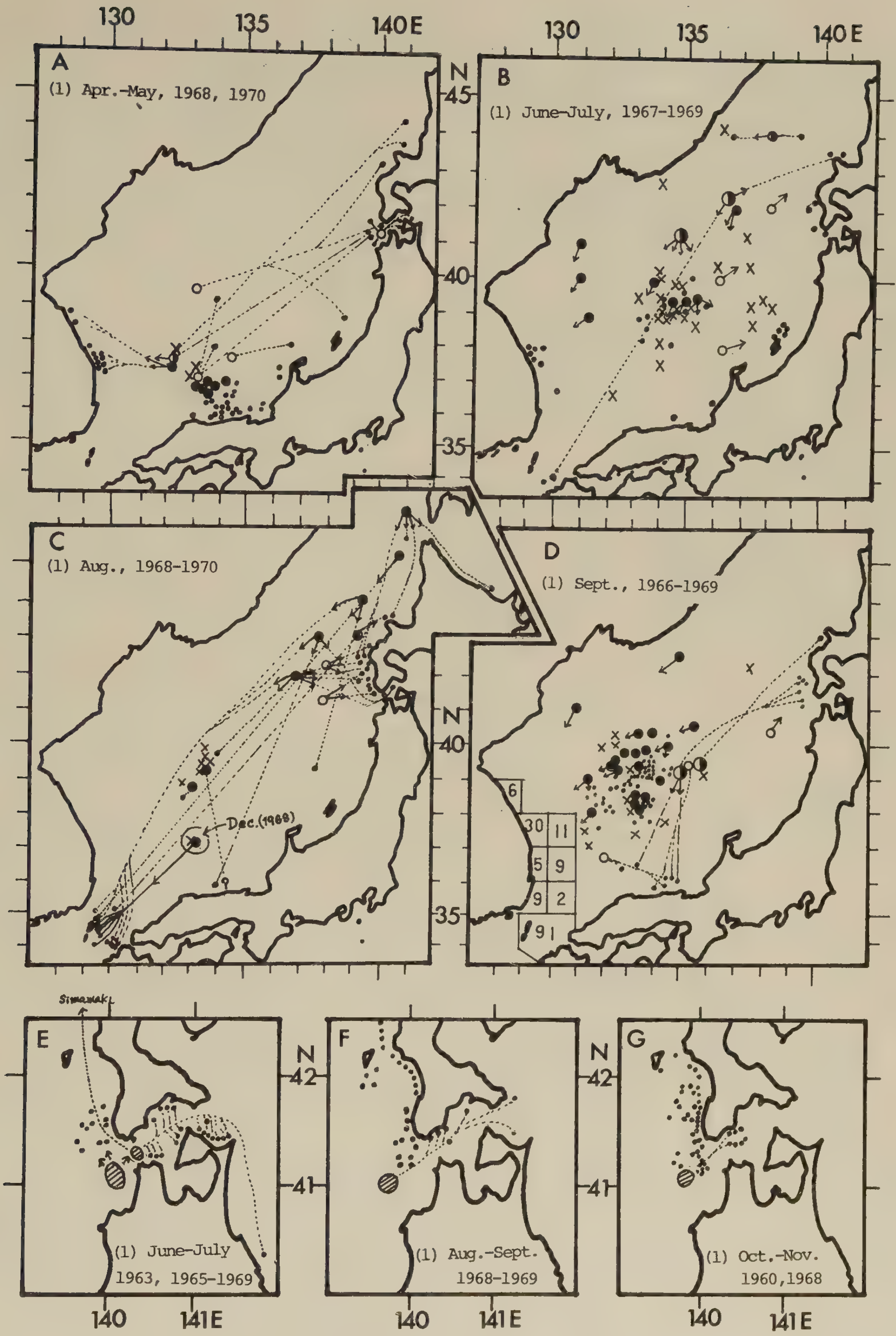

130
135
140E
A
(1) Apr.-May, 1968, 1970
B
(1) June-July, 1967-1969
N
45
40
35
C
(1) Aug., 1968-1970
Dec.(1968)
D
(1) Sept., 1966-1969
6
30
11
5
9
9
2
91
Simamaki
E
(1) June-July
1963, 1965-1969
F
(1) Aug.-Sept.
1968-1969
G
(1) Oct.-Nov.
1960,1968
42
41
140
141E

Fig. 17-1 Movement of tagged *Todarodes pacificus* released in the Japan Sea (based on Japan Sea Reg. Fish. Res. Lab. (ed), 1977)

(1) : Month and year released
A-D : ● Southward or westward movement
○ Northward or eastward movement
◐ Movement in all directions
× Released point with no squid recaptured
• Point recaptured
Figures in panel D indicate no. of squid recaptured (total: 247)
E-G : ▨ Area released
• Point recaptured

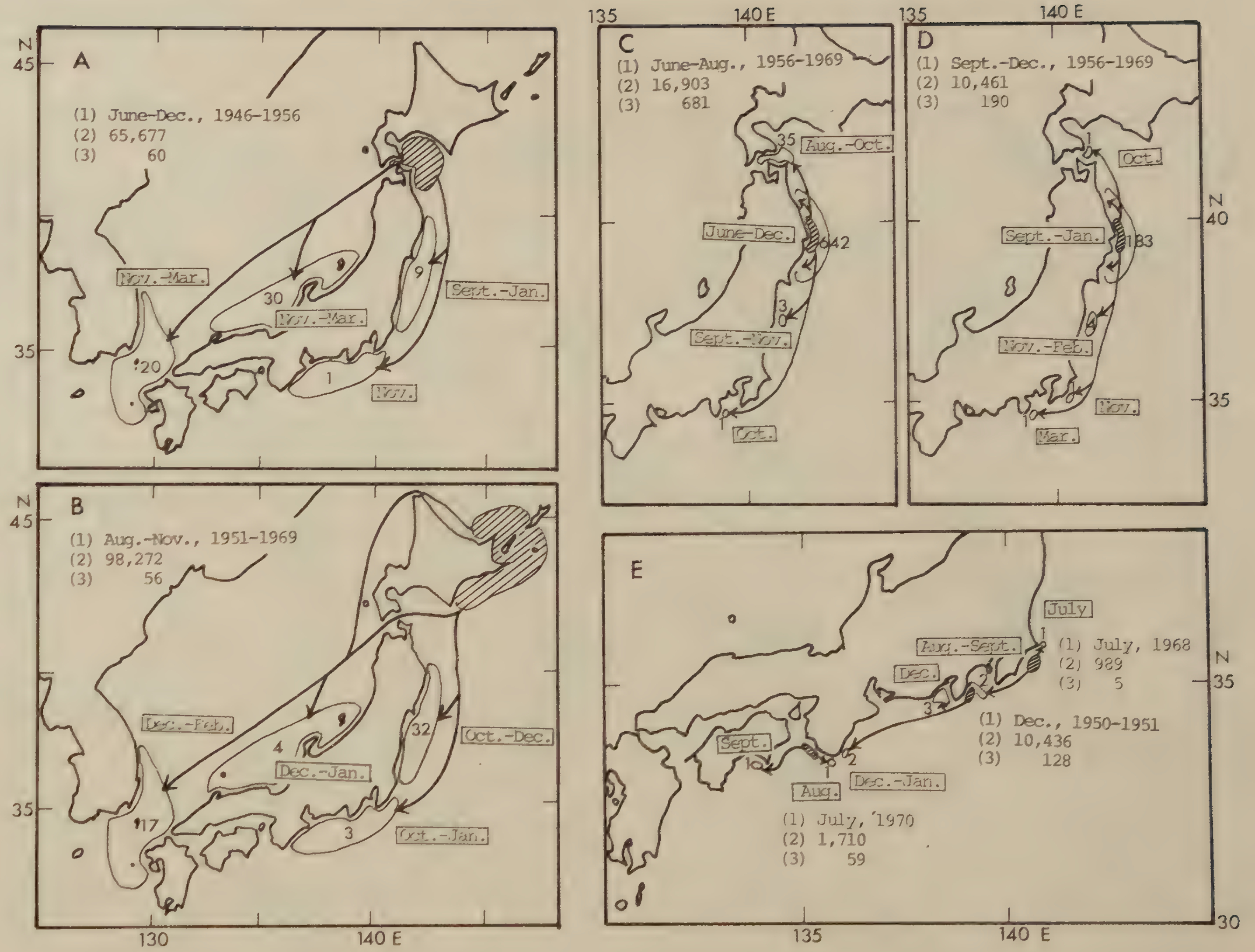

A
(1) June-Dec., 1946-1956
(2) 65,677
(3) 60
Nov.-Mar.
30
Nov.-Mar.
9
Sept.-Jan.
20
1
Nov.
B
(1) Aug.-Nov., 1951-1969
(2) 98,272
(3) 56
Dec.-Feb.
4
Dec.-Jan.
32
Oct.-Dec.
17
3
Oct.-Jan.
C
(1) June-Aug., 1956-1969
(2) 16,903
(3) 681
35
Aug.-Oct.
June-Dec.
642
3
Sept.-Nov.
1
Oct.
D
(1) Sept.-Dec., 1956-1969
(2) 10,461
(3) 190
1
Oct.
Sept.-Jan.
183
Nov.-Feb.
Nov.
1
Mar.
E
July
(1) July, 1968
(2) 989
(3) 5
Aug.-Sept.
Dec.
3
(1) Dec., 1950-1951
(2) 10,436
(3) 128
Sept.
1
2
Aug.
Dec.-Jan.
(1) July, 1970
(2) 1,710
(3) 59
N
45
35
40
30
130
135
140 E

Figure 17-2 Movement of tagged *Todarodes pacificus* released in the Pacific and the Okhotsk Sea (A-B: data from Hokkaido Reg. Fish. Res. Lab.; C-E: based on Tech. Con. Min. Agr. For. Fish., 1972 and Kawana, Takemura and Yamane, 1970)

▨ Area released
○ Area recaptured

(1) Month and year released
(2) Total number of tagged squid
(3) Total number of squid recaptured

(Figure) Number of squid recaptured in this area
▭ Month recaptured

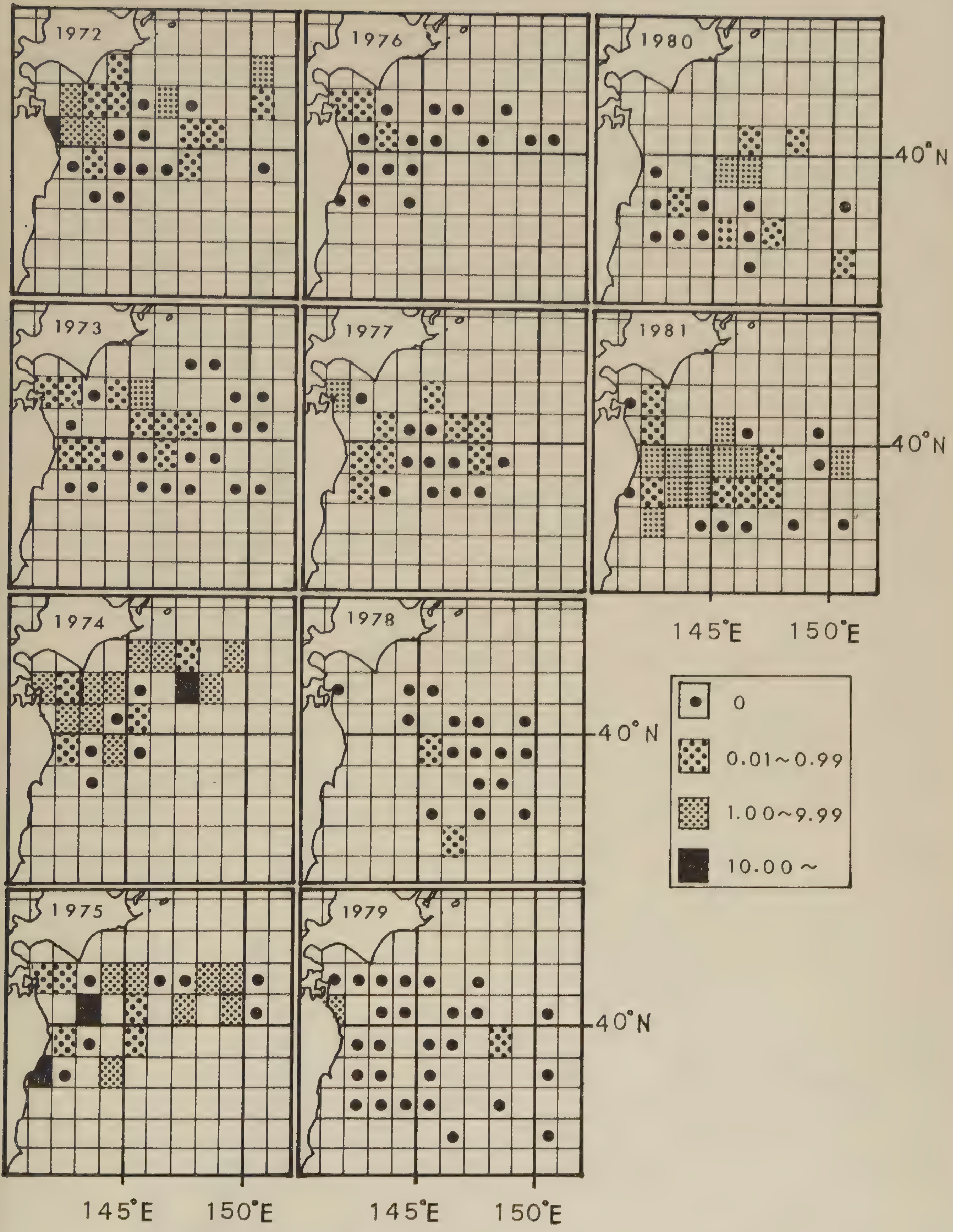

1972
1976
1980
1973
1977
1981
1974
1978
1975
1979
40°N
40°N
40°N
40°N
145°E
150°E
145°E
150°E
145°E
150°E
● 0
0.01~0.99
1.00~9.99
10.00 ~

Fig. 18 Distributions of average CPUE (catch-per-jigger-per-hour in number) of *Todarodes pacificus* by 1° square, in the spring fishing season, 1972-81

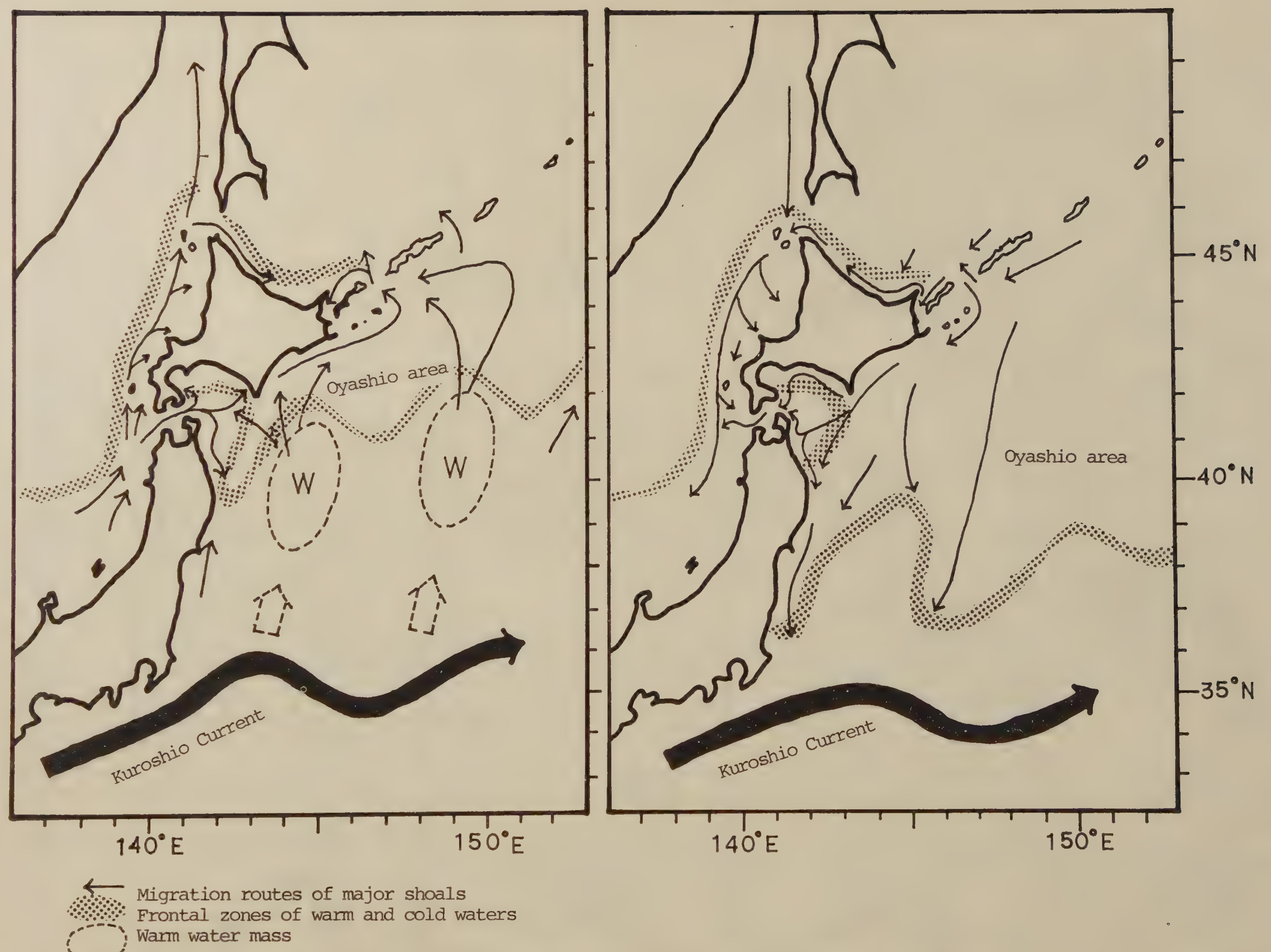

Oyashio area
W
W
Kuroshio Current
140°E
150°E
Oyashio area
Kuroshio Current
140°E
150°E
45°N
40°N
35°N
Migration routes of major shoals
Frontal zones of warm and cold waters
Warm water mass

Fig. 19 Northward and southward migration of winter population of *Todarodes pacificus* (Araya, 1976)

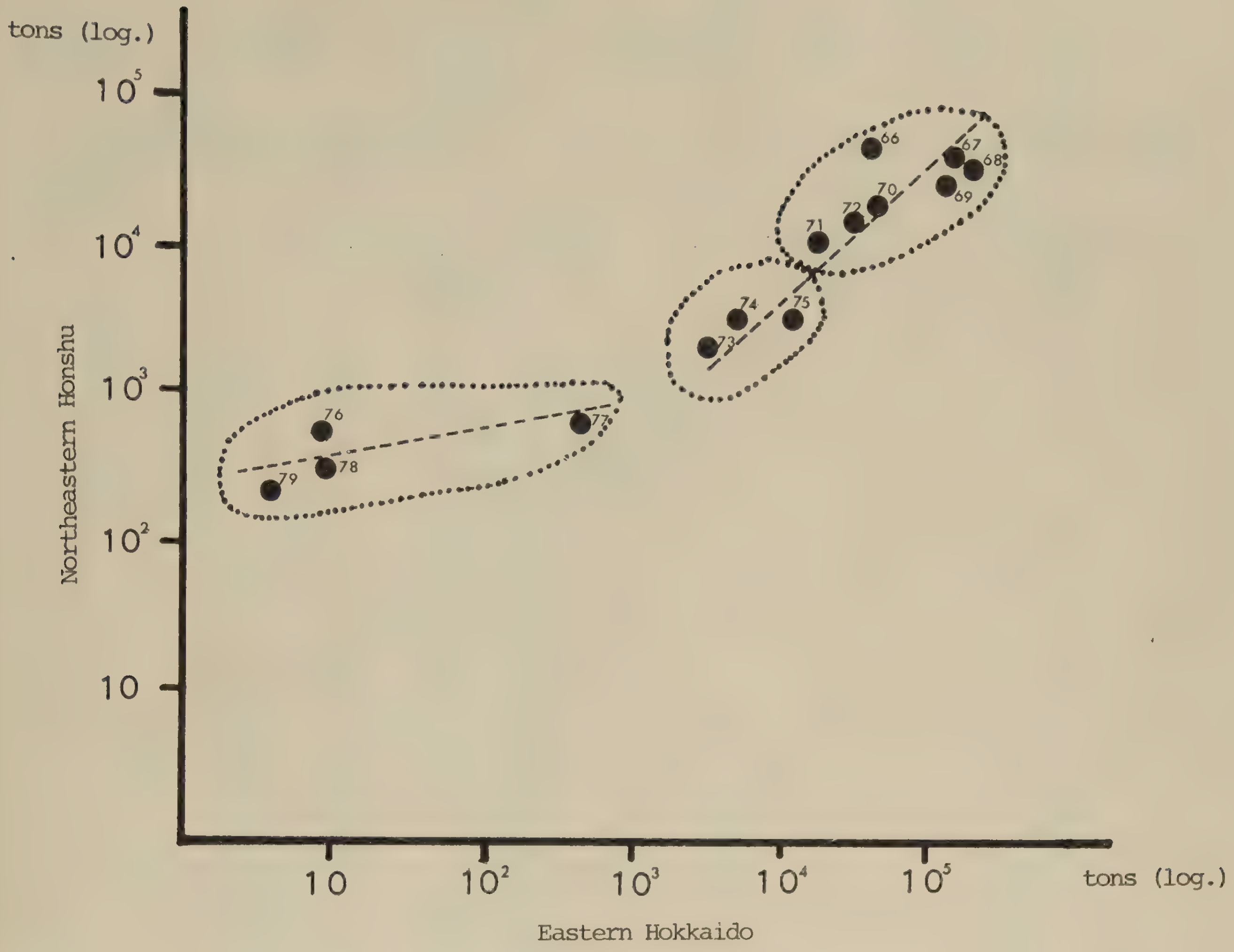


Fig. 20 Relation between catches from northeastern Honshu (Oct.-Jan.) and from eastern Hokkaido (May-Sep.) (data from Iwate Pref. Fis. Expe. St., mimeo)

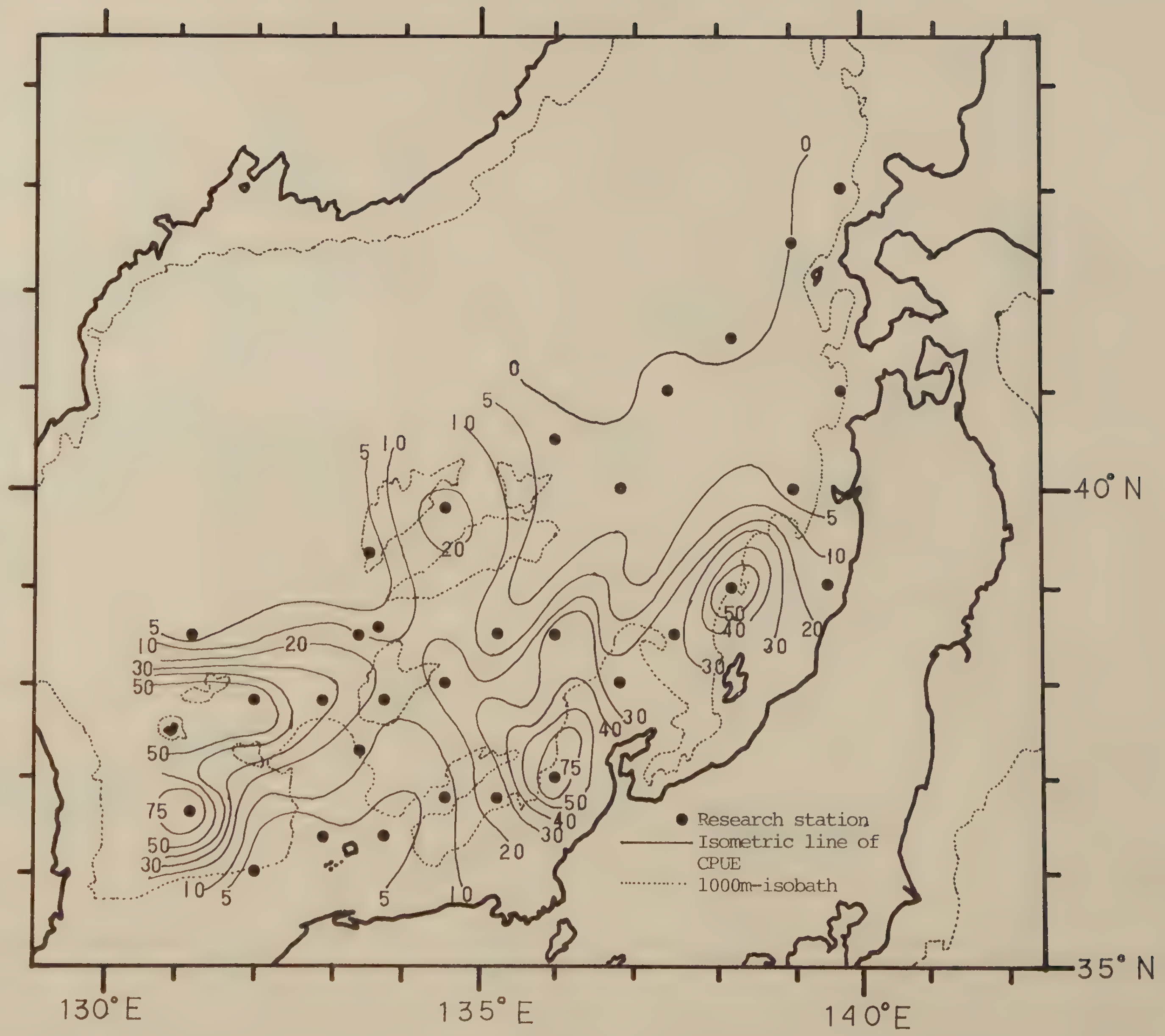

40° N
35° N
130°E
135°E
140°E
Research station
Isometric line of CPUE
1000m-isobath
0
5
10
20
30
40
50
75

Fig. 21 Distribution-densities (in terms of CPUE) of *Todarodes pacificus* in June of 1980 in the Japan Sea (data from Japan Sea Reg. Fish. Res. Lab.)
CPUE: Catch-per-jigger-per-hour in number

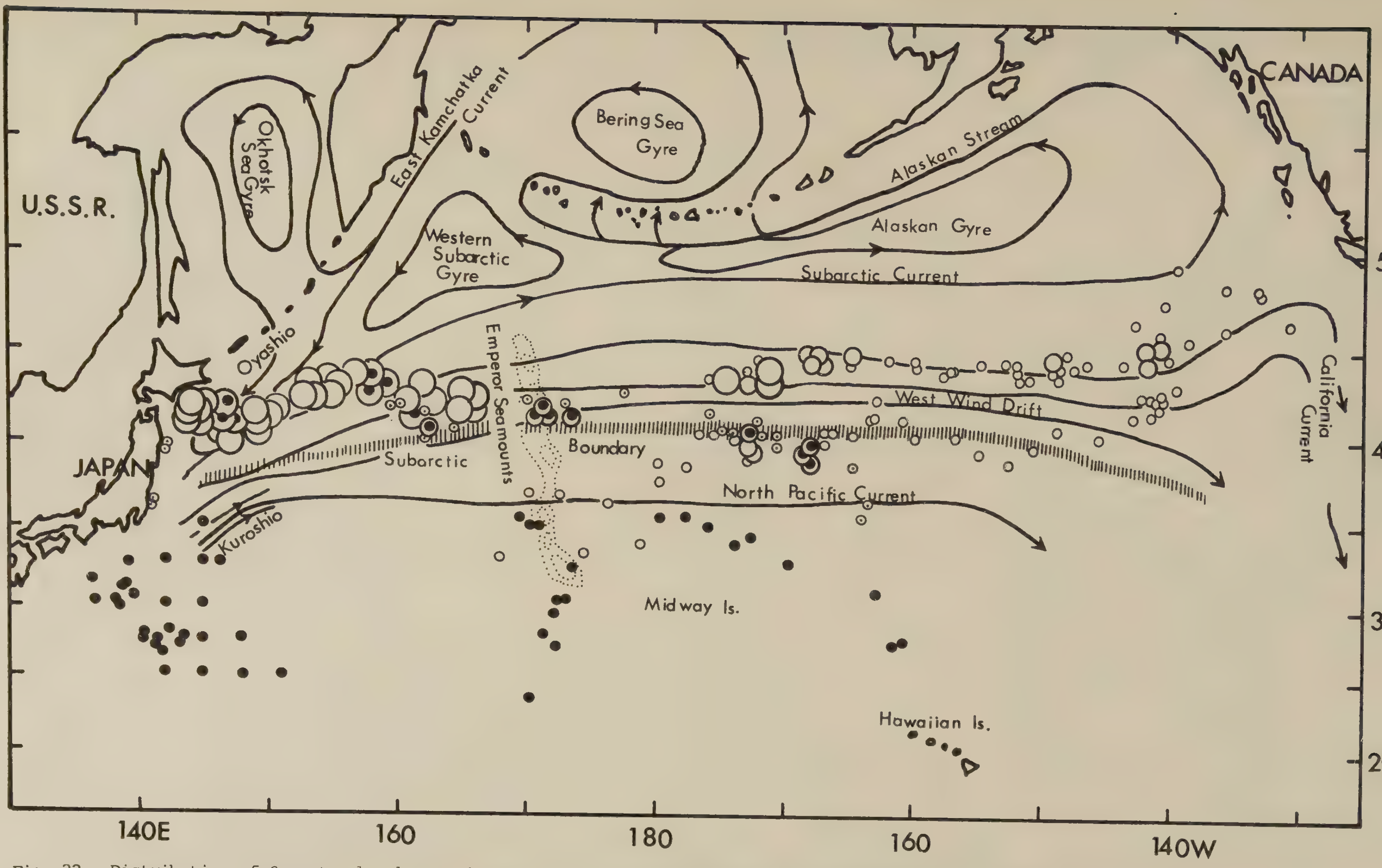

U.S.S.R.
CANADA
JAPAN
Okhotsk Sea Gyre
East Kamchatka Current
Bering Sea Gyre
Alaskan Stream
Alaskan Gyre
Western Subarctic Gyre
Subarctic Current
Oyashio
Emperor Seamounts
West Wind Drift
California Current
Subarctic
Boundary
North Pacific Current
Kuroshio
Midway Is.
Hawaiian Is.
50N
40
30
20
140E
160
180
160
140W

Fig. 22 Distribution of *Ommastrephes bartrami* in the north Pacific during the year from June 1978 to February 1980 (Murakami, Watanabe and Nakata, 1981)

Migration: ○ Northward migration (June-Sept.)
⊙ Southward migration (Oct.-Dec.)
• Spawning migration (Jan.-May)

Catch per jigging through one night:
o below 1 t ◯ 1-2.9 t ◯ over 3 t

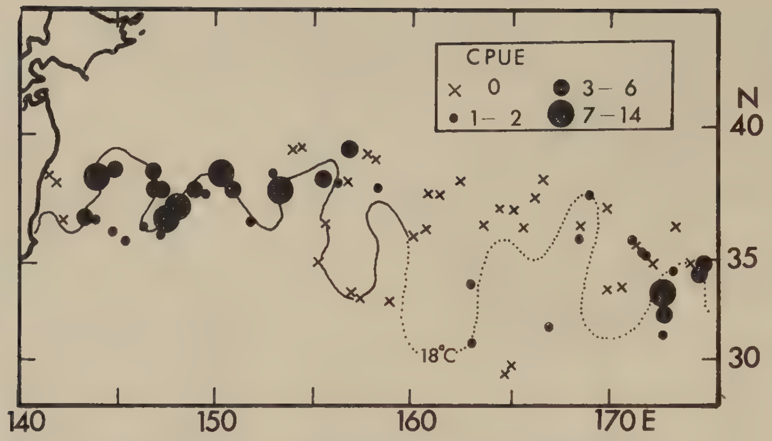

CPUE
× 0
● 1– 2
● 3– 6
● 7–14
N
40
35
30
18°C
140
150
160
170 E

Fig. 23 Distribution of *Ommastrephes bartrami* in May and June of 1977 (data from Aomori Prefecture Fishery Experimental Station)
CPUE: number of squid caught-per-jigger-per-hour

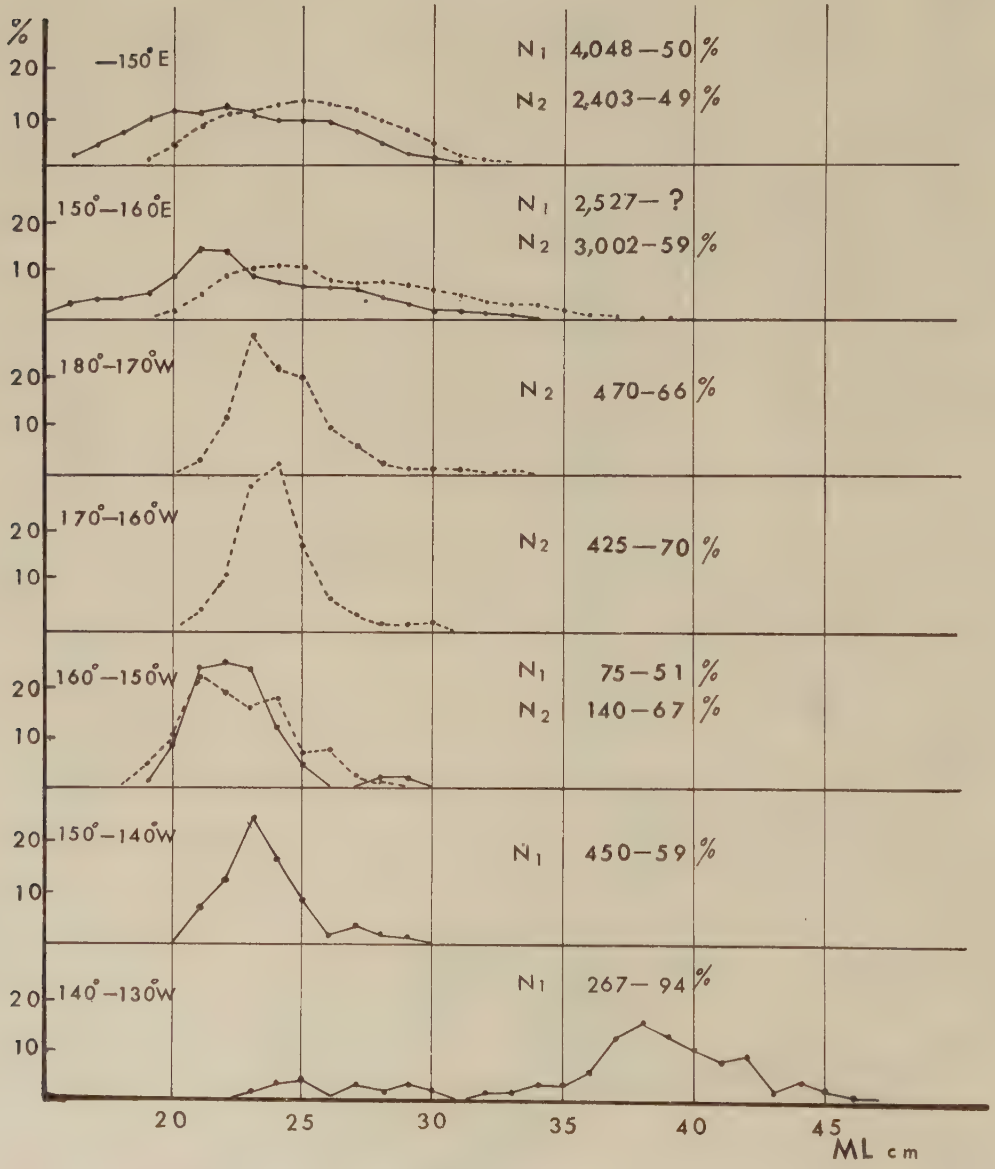


Fig. 24 Dorsal mantle length compositions by waters of *Ommastrephes bartrami* caught by jigging in the north Pacific in 1979
•————• August (N_1) .-------------. September (N_2)
N: number of squid —— percentage of females

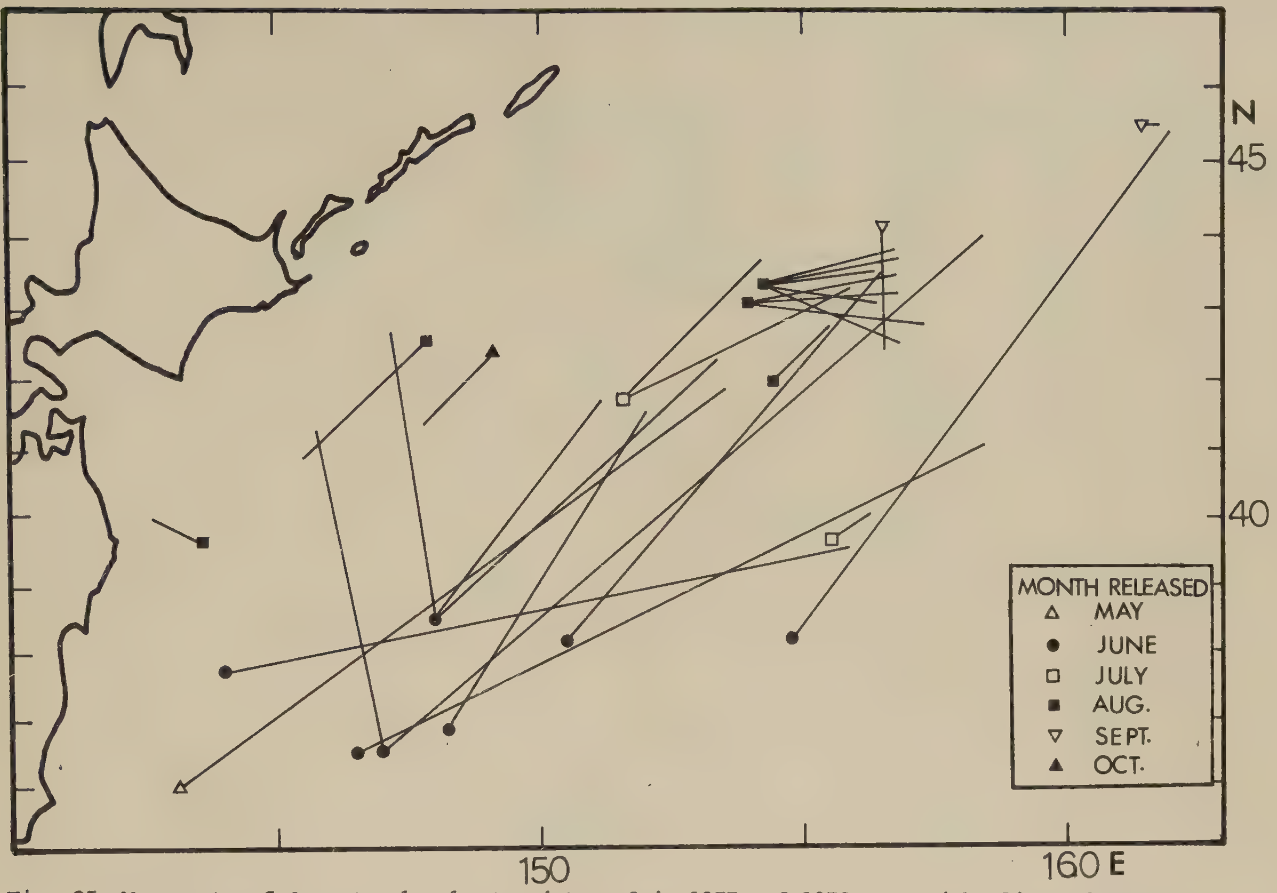

N
45
40
150
160 E
MONTH RELEASED
△ MAY
● JUNE
□ JULY
■ AUG.
▽ SEPT.
▲ OCT.

Fig. 25 Movements of *Ommastrephes bartrami* tagged in 1977 and 1978 - Straight lines show ones connecting the points of release and recapture (data from Japan Marine Fishery Resource Center, Aomori Prefecture Fishery Experimental Station and Hokkaido Reg. Fish. Res. Lab.)

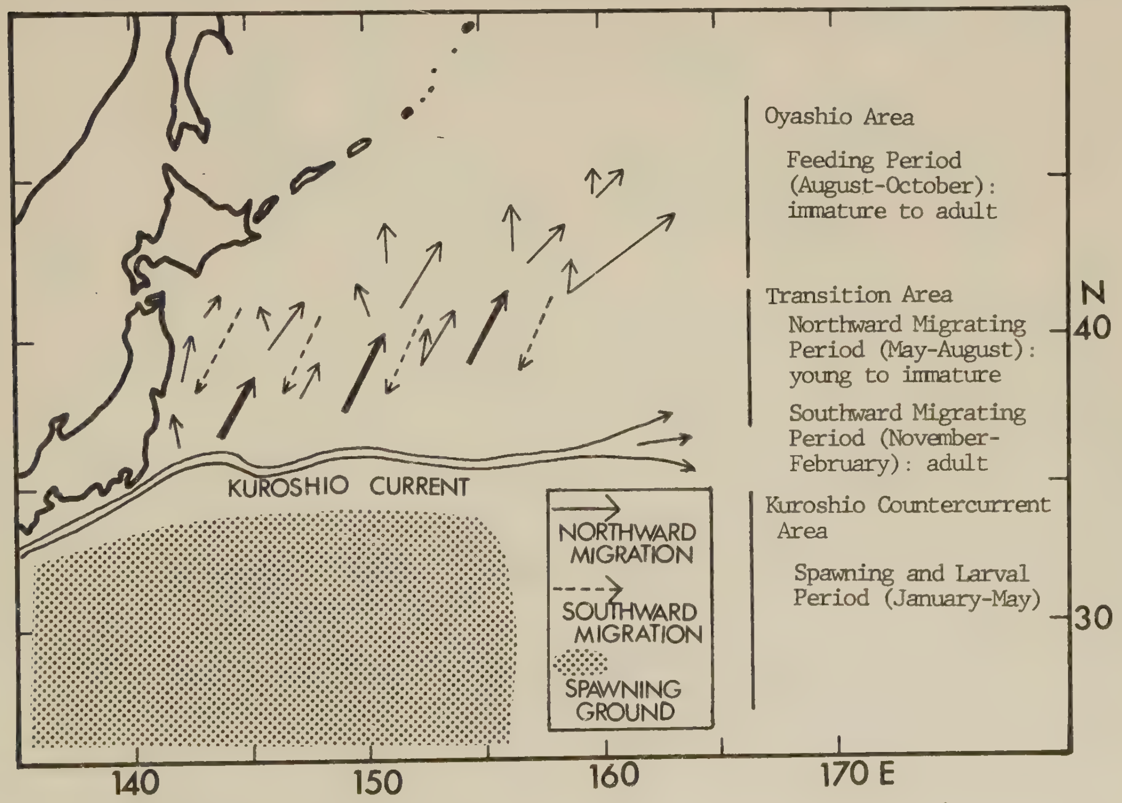

Oyashio Area
Feeding Period (August-October): immature to adult
Transition Area
Northward Migrating Period (May-August): young to immature
Southward Migrating Period (November-February): adult
Kuroshio Countercurrent Area
Spawning and Larval Period (January-May)
KUROSHIO CURRENT
NORTHWARD MIGRATION
SOUTHWARD MIGRATION
SPAWNING GROUND
N
40
30
140
150
160
170 E

Fig. 26 Schematic illustration showing migration of *Ommastrephes bartrami*

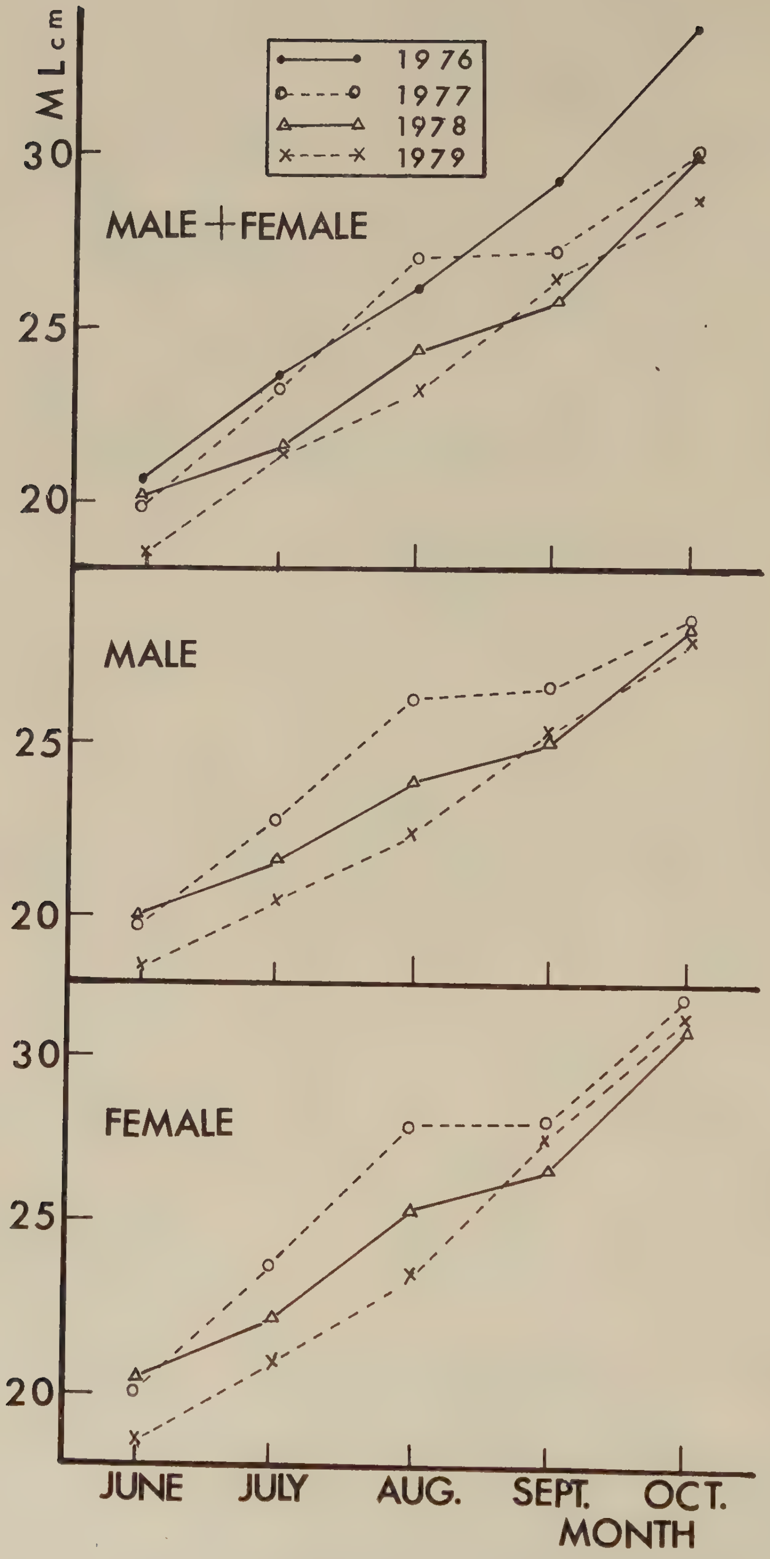


Fig. 27 Monthly average of dorsal mantle length (ML) of *Ommastrephes bartrami* caught by jigging in waters west of 160°E

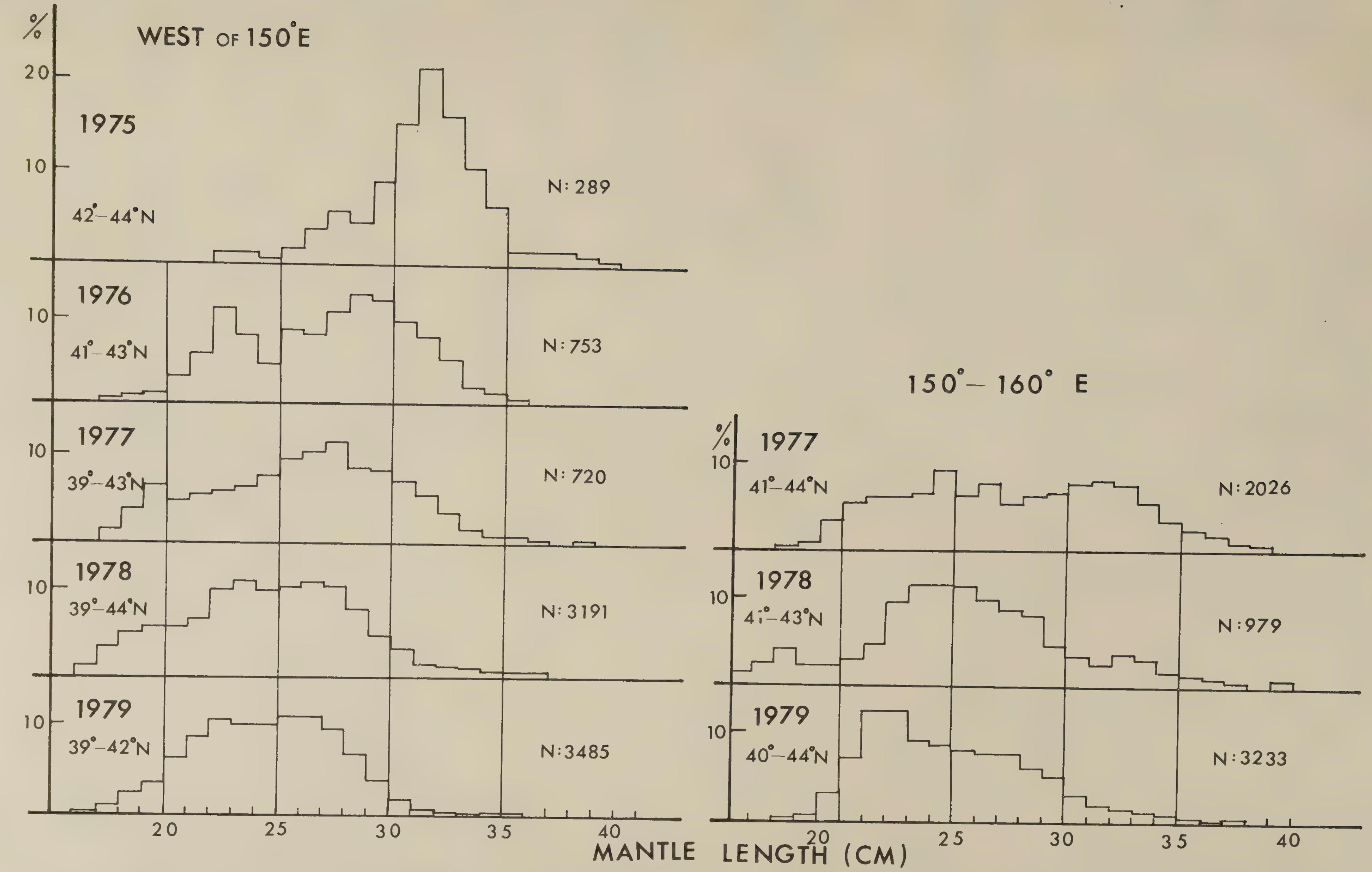


Fig. 28 Periodic change in the annual dorsal mantle length compositions of *Ommastrephes bartrami* caught by jigging in the period of late August to early September 1975-79
N: number of squid

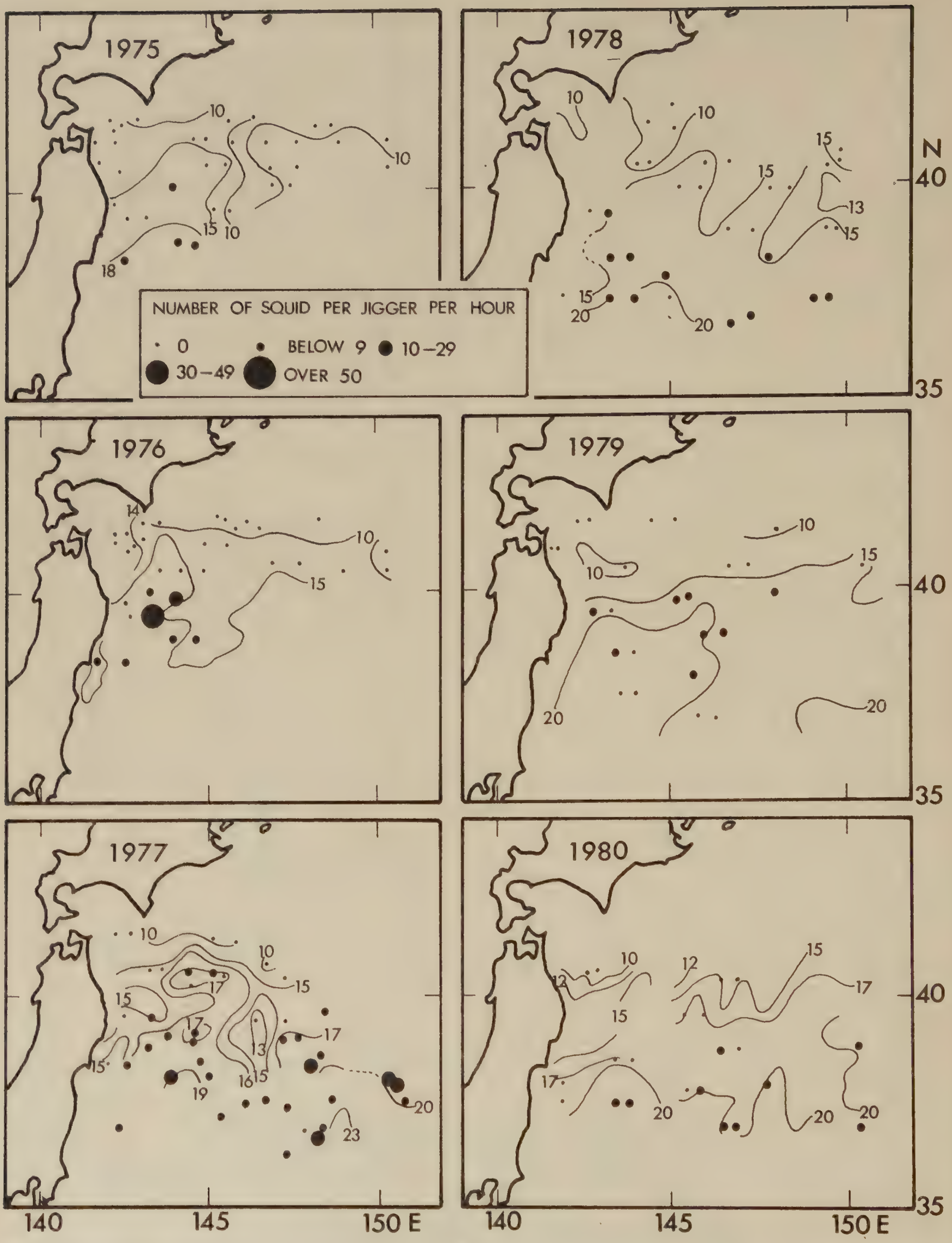

1975
1978
1976
1979
1977
1980
NUMBER OF SQUID PER JIGGER PER HOUR
· 0
• BELOW 9
● 10–29
● 30–49
● OVER 50
10
15
13
17
18
20
23
N
40
35
140
145
150 E

Fig. 29 Number of *Ommastrephes bartrami* caught-per-jigger-per-hour in the grid surveys in June
Solid line: surface water temperature (°C)

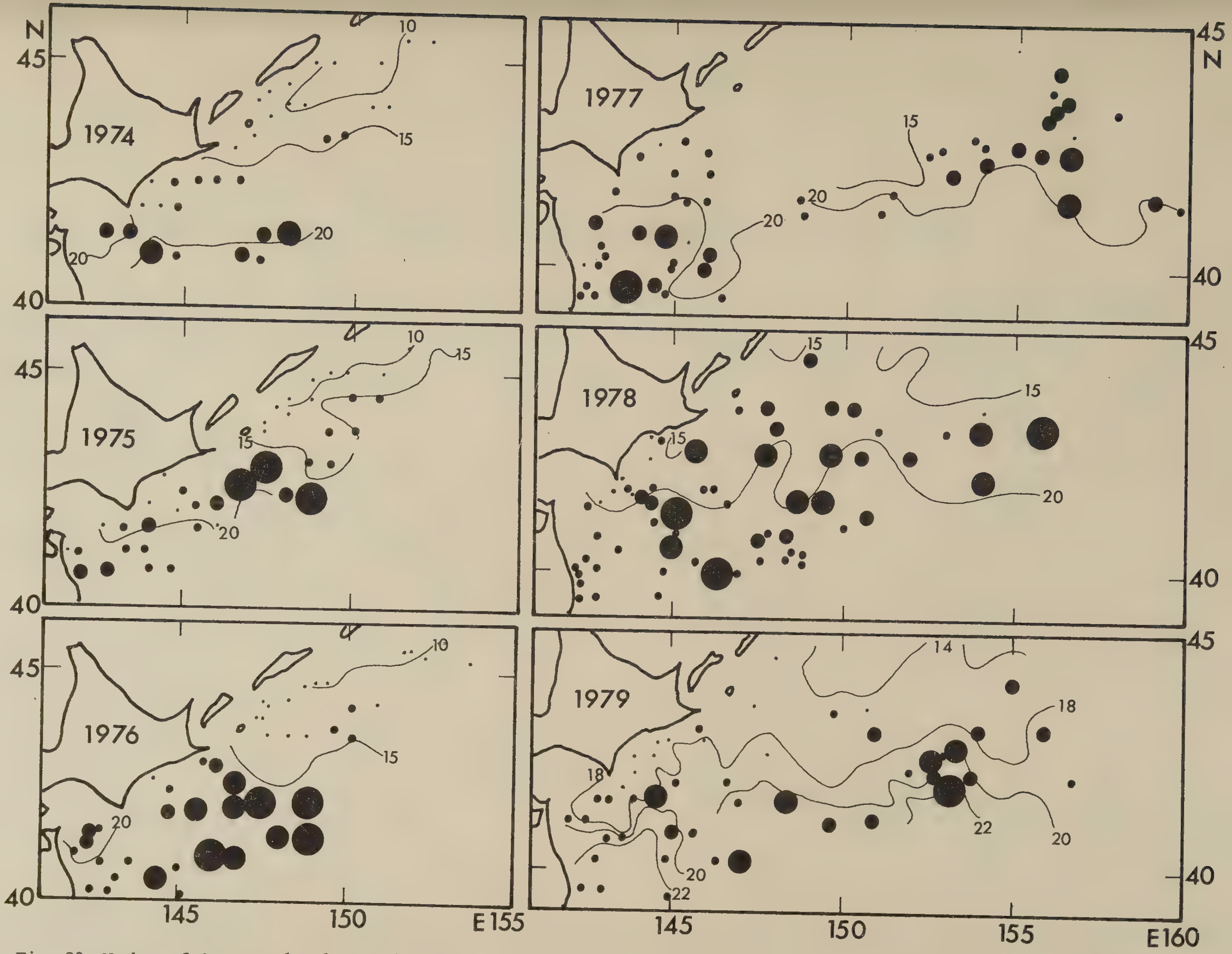

1974
1975
1976
1977
1978
1979
10
15
20
14
18
22
N
45
40
145
150
E155
155
E160

Fig. 30 Number of *Ommastrephes bartrami* caught-per-jigger-per-hour in the grid surveys from late August to early September (see Fig. 29 for legend)

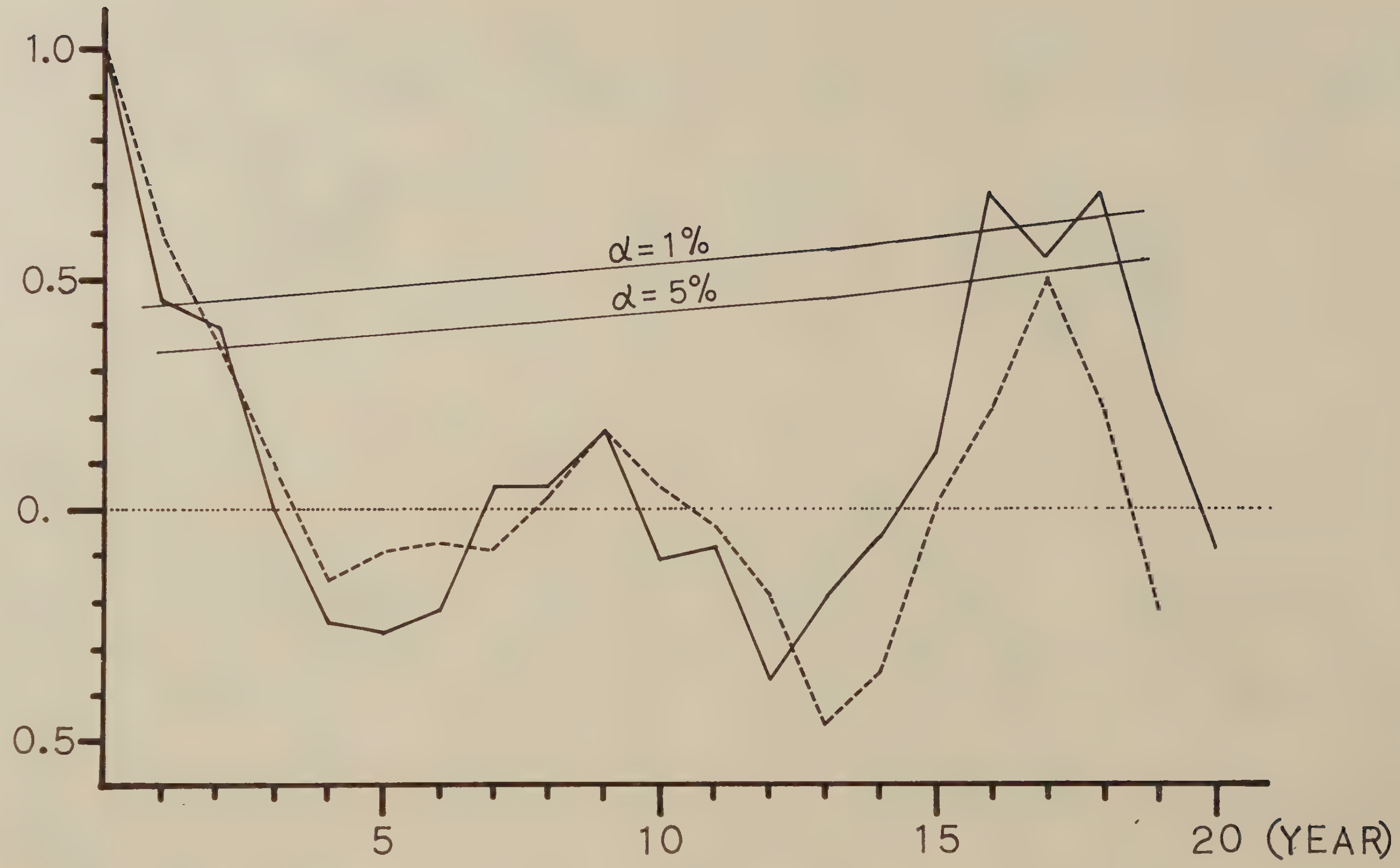


Fig. 31 Corerogram of catch of *Todarodes pacificus* (winter population) (Murata, 1977)
——— 1910-41; -------- 1947-76

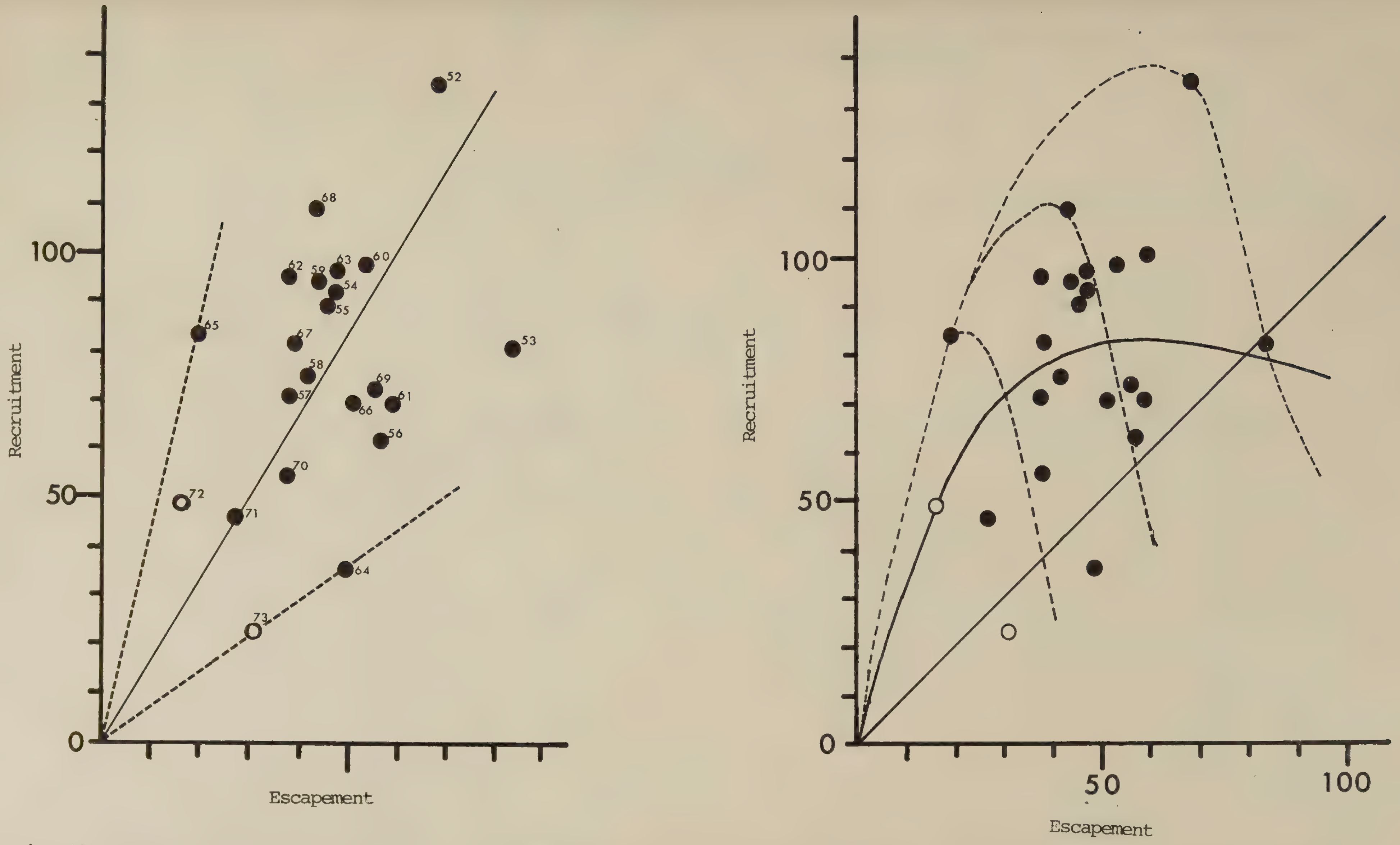
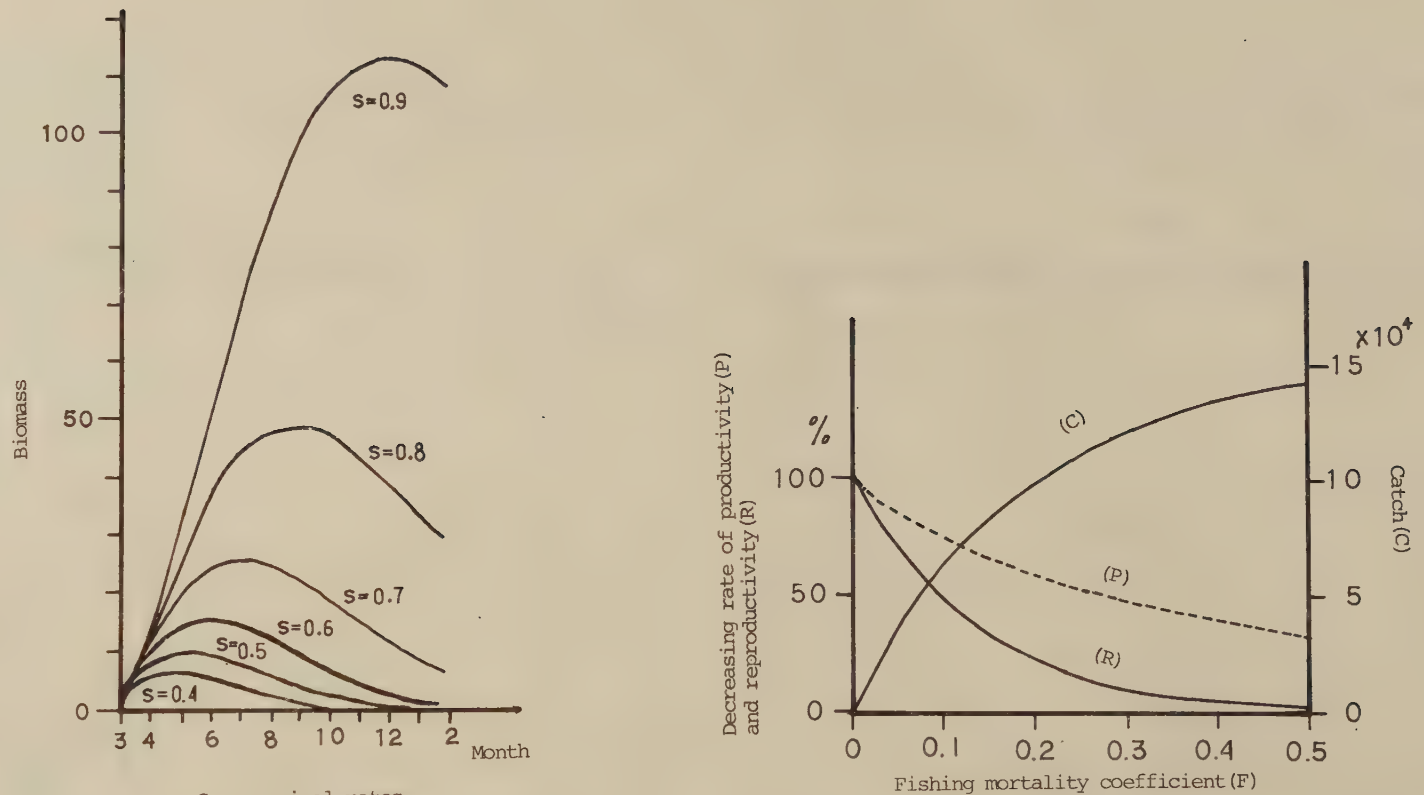


Fig. 32 Relation between the parents and recruitment of *Todarodes pacificus* in the waters off Japan and reproductive curves applied to Ricker's form (Araya, 1974)



S: survival rates

Population in number by age (in month) : $N_t = \begin{cases} N_3 e^{-M(t-3)} & 3 \leq t \leq 6 \\ N_3 e^{-3M} e^{-(M+F)(t-6)} & 6 \leq t \leq 14 \end{cases}$

Population in weight = $N_t W_t$

Catch : $C = \Sigma N_t W_t$

Spawning population = $\frac{1}{2}(N_{13} + N_{14})$

Decreasing rate of reproductivity = $\frac{\text{Spawning population}}{\text{Spawning population in virgin stock}}$

Productivity = $\frac{C}{F}$

Fig. 33 Analyses of biomass (for winter population in the Japan Sea) and percussion of the fishery stock (Doi and Kawakami, 1979)

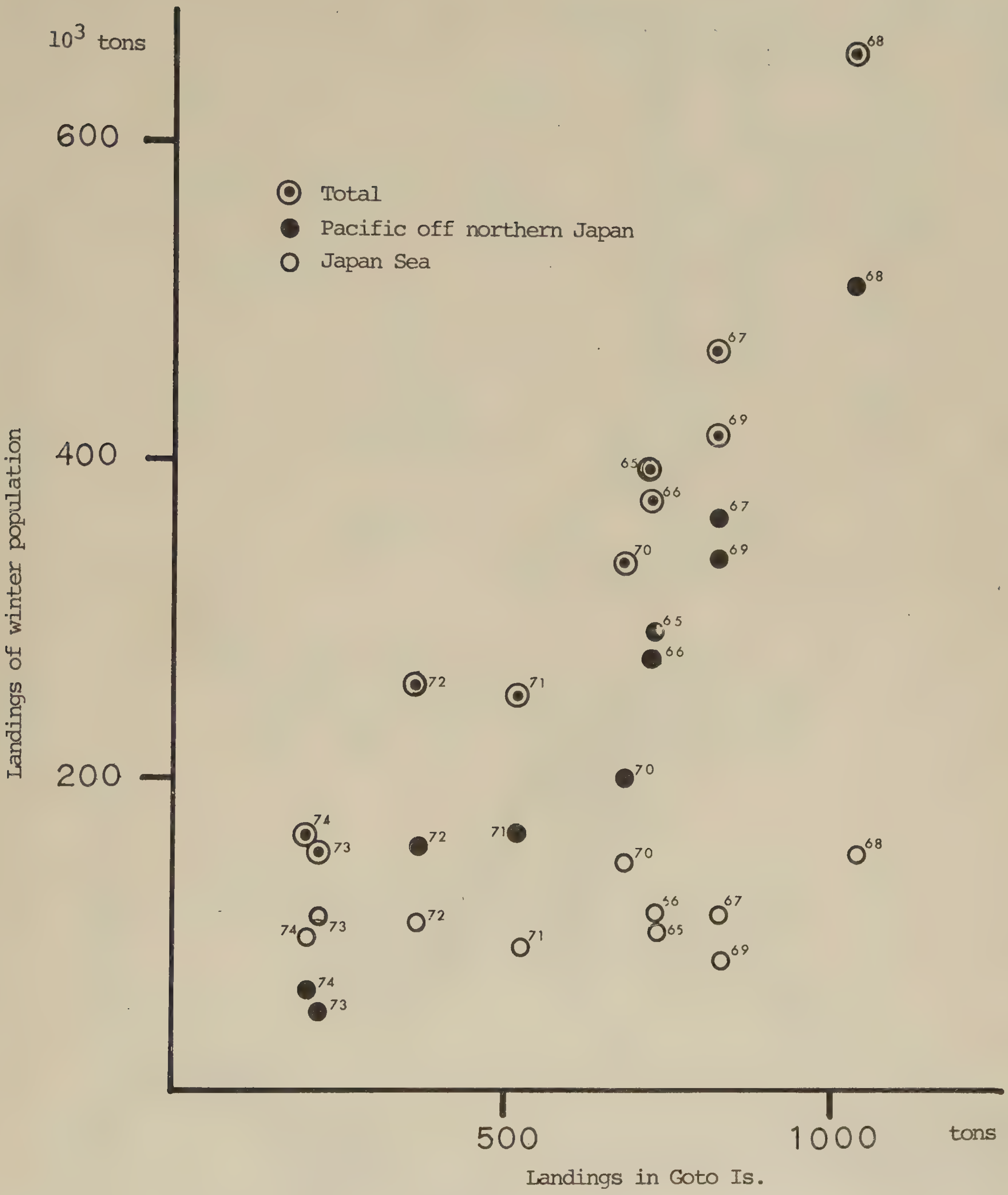


Fig. 34 Relation between landings (Jan.-Feb.) at four major ports in Goto Is. and landings of winter population (*Todarodes pacificus*) in the Japan Sea and Pacific off northern Japan (Doi and Kawakami, 1979)

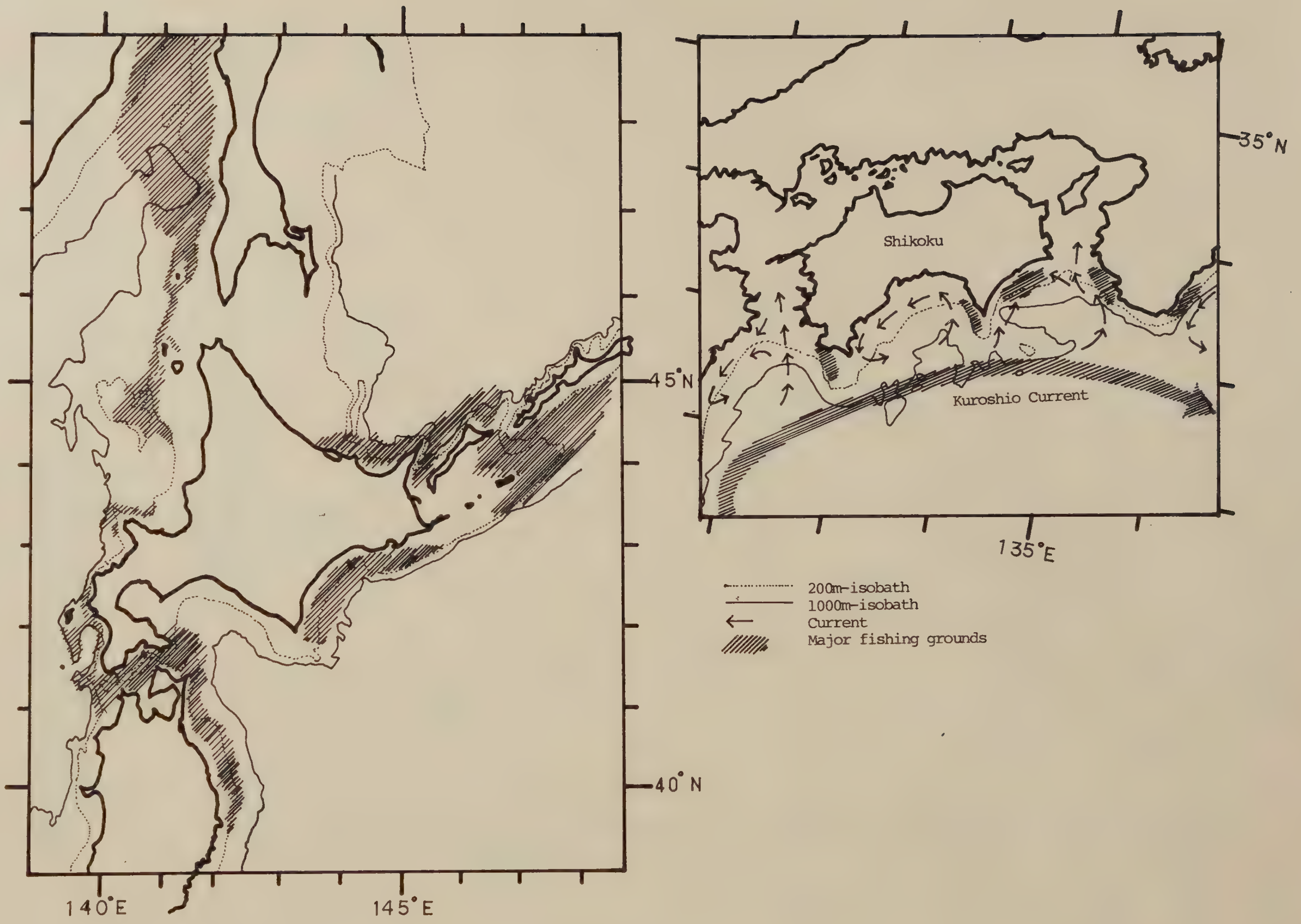

35°N
45°N
40°N
140°E
145°E
135°E
Shikoku
Kuroshio Current
200m-isobath
1000m-isobath
Current
Major fishing grounds

Fig. 35 Topographical features of sea bottoms around the major fishing grounds for *Todarodes pacificus*

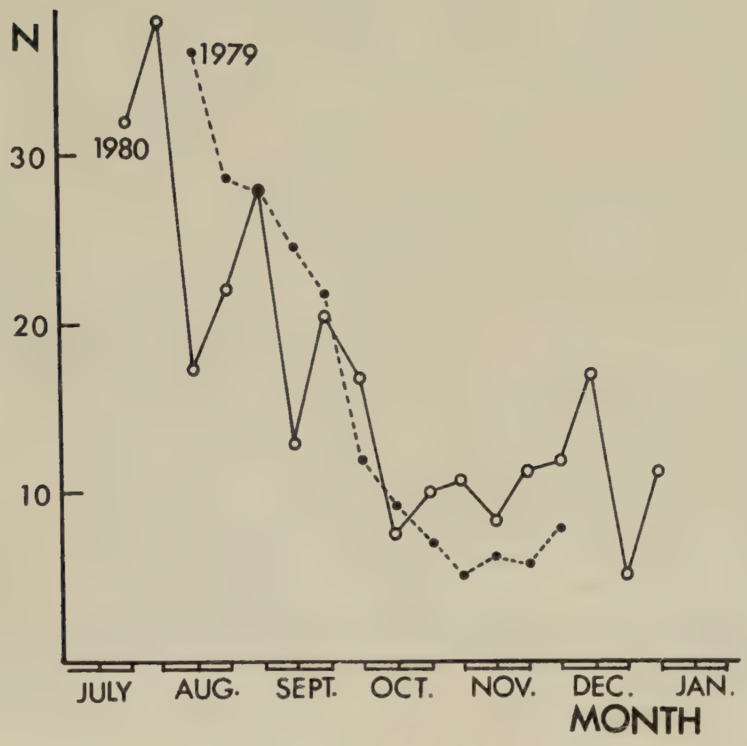
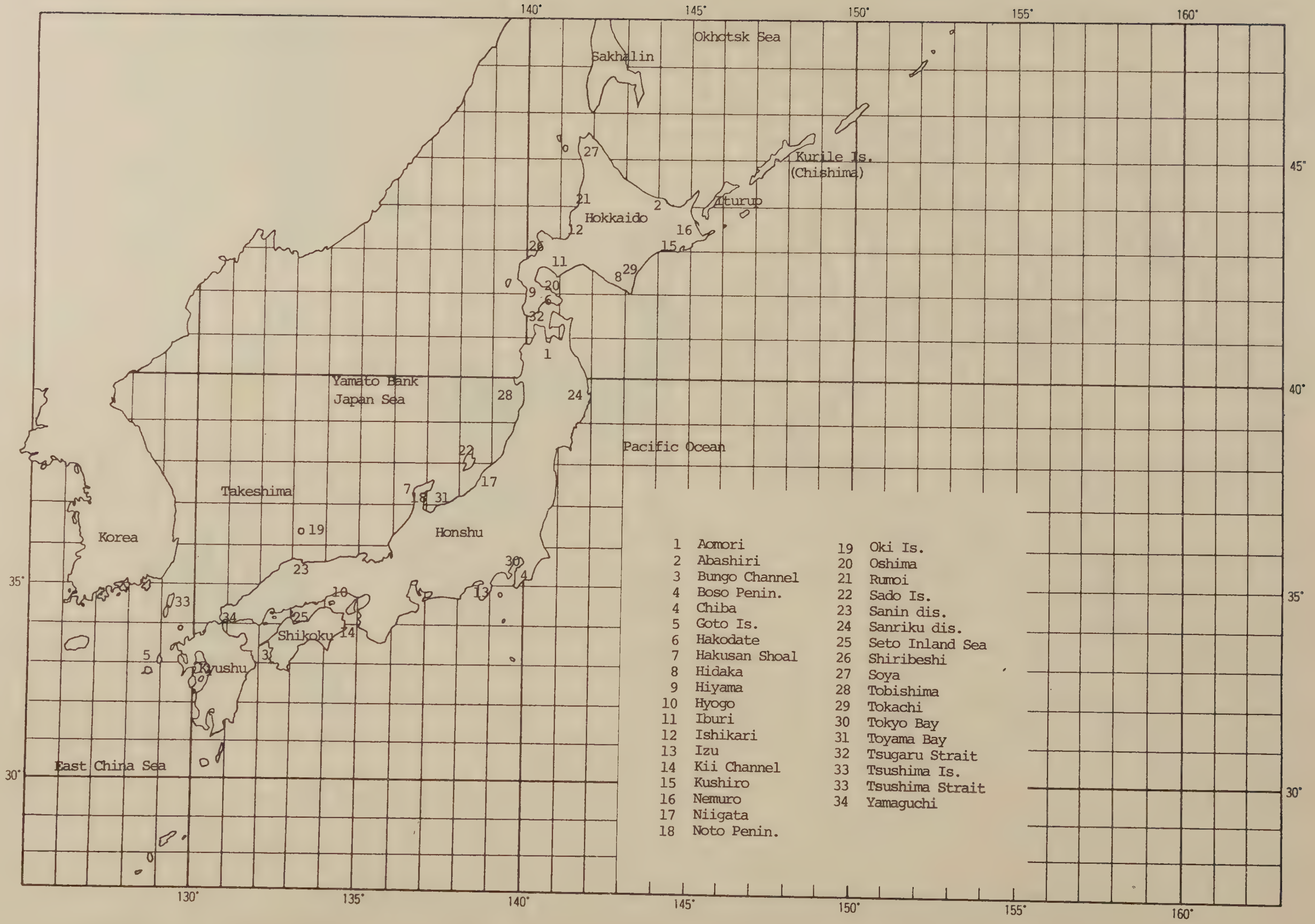


Fig. 36 Seasonal change in number of *Ommastrephes bartrami* caught-per-jigger-per-hour (N) by large-sized boats (over 100 t) in 1979 and 1980 (Aomori Pre. Fish. Exp. St.)


140°
145°
150°
155°
160°
45°
40°
35°
30°
130°
135°
Okhotsk Sea
Sakhalin
Kurile Is.
(Chishima)
Iturup
Hokkaido
Yamato Bank
Japan Sea
Pacific Ocean
Takeshima
Korea
Honshu
Shikoku
Kyushu
East China Sea
1 Aomori
2 Abashiri
3 Bungo Channel
4 Boso Penin.
4 Chiba
5 Goto Is.
6 Hakodate
7 Hakusan Shoal
8 Hidaka
9 Hiyama
10 Hyogo
11 Iburi
12 Ishikari
13 Izu
14 Kii Channel
15 Kushiro
16 Nemuro
17 Niigata
18 Noto Penin.
19 Oki Is.
20 Oshima
21 Rumoi
22 Sado Is.
23 Sanin dis.
24 Sanriku dis.
25 Seto Inland Sea
26 Shiribeshi
27 Soya
28 Tobishima
29 Tokachi
30 Tokyo Bay
31 Toyama Bay
32 Tsugaru Strait
33 Tsushima Is.
33 Tsushima Strait
34 Yamaguchi

A REVIEW OF ASSESSMENT OF JAPANESE DISTANT-WATER FISHERIES FOR CEPHALOPODS

by

T. Sato and H. Hatanaka
Far Seas Fisheries Research Laboratory
Shimizu, Japan

ABSTRACT

This historical progress of Japanese distant-water fisheries for cephalopods and the state of some important cephalopod stocks fished by Japan is reviewed. The total Japanese annual catch of cephalopods has been maintained at about 110 000 t in recent years, which includes 14 commercially important species of squid, cuttlefish and octopus from seven FAO fishing areas. Preliminary stock studies have been made on seven species from six areas, and with the exception of the *Illex* and *Loligo* squid in American and Canadian waters, the current status of five species, namely *Loligo*, *Nototodarus* and *Illex* squid in South African, New Zealand and Argentine waters, respectively, octopus off northwestern Africa, and cuttlefishes off the P.D.R. of Yemen are reviewed in this paper. As for most cephalopods fished by Japan, however, the lack of knowledge on the stock-recruitment relationship and the wide-ranging year-to-year fluctuations of catchable populations have made it difficult to apply analytical models to the stock assessment. Stock studies on those stocks have therefore laid stress on biomass estimation by means of the areal expansion method as the best way available for the time being of estimating population size, and potential yield results obtained suggest that fisheries for the three species of squid have not yet been fully exploited, although wide variation in annual recruitment made it difficult to specify one fixed level of sustainable yield for these short-lived species.

RESUME

On fait l'historique des pêcheries hauturières de céphalopodes au Japon et étudié l'état de certains stocks importants qui y sont exploités. Les captures totales de céphalopodes au Japon ont été maintenues à environ 110 000 t par an ces dernières années et touchent 14 espèces, importantes du point de vue commercial, de calamars, seiches et pieuvres provenant de sept zones de pêche de la FAO. Des études préliminaires sur les stocks ont été effectuées sur sept espèces provenant de six zones et on étudie dans le présent document la situation actuelle de cinq espèces (à l'exception des calamars *Illex* et *Loligo* dans les eaux américaines et canadiennes, notamment les calamars *Loligo*, *Nototodarus* et *Illex* présents dans les eaux d'Afrique du Sud, de Nouvelle-Zélande et d'Argentine respectivement, des pieuvres qui se trouvent au large des côtes de l'Afrique du Nord-Ouest et des seiches qui sont au large des côtes de la République démocratique populaire du Yémen. Comme pour la plupart des céphalopodes pêchés par le Japon, cependant, le manque de renseignements sur le rapport stock-recrutement et les fortes fluctuations d'un année sur l'autre des populations pouvant être capturées ont rendu difficile l'application de modèles analytiques pour l'évaluation des stocks. Cependant, les études concernant ces stocks ont mis l'accent sur l'estimation de la biomasse au moyen de la méthode d'expansion zonale qui est actuellement la meilleure pour estimer la taille des peuplements et le rendement potentiel. D'après les résultats obtenus, les pêcheries pour les trois espèces de céphalopodes considérées n'ont pas encore été pleinement exploitées bien que les fortes variations qui existent dans le recrutement annuel permettent difficilement de fixer un niveau de rendement continu pour ces trois espèces.

RESUMEN

Se examina el progreso evolutivo de la pesca japonesa de gran altura de cefalópodos y la situación de algunas poblaciones importantes de cefalópodos capturados por el Japón. La captura anual japonesa de cefalópodos, cuyo volumen total en los últimos años se ha mantenido alrededor de las 110 000 t, comprende 14 importantes especies comerciales de calamares, sepias y pulpos, procedentes de siete áreas de pesca de la FAO. Se han efectuado estudios preliminares de población sobre siete especies de seis áreas y, a excepción de los calamares *Illex* y *Loligo* en aguas americanas y canadienses, en este documento se examina la situación actual de cinco especies, a saber, los calamares *Loligo*, *Nototodarus* e *Illex* en aguas sudafricanas, neozelandesas y argentinas respectivamente, el pulpo en aguas litorales del noroeste de Africa, y la sepia en aguas litorales de la República Democrática Popular del Yemen. Sin embargo, como ocurre con la mayoría de los cefalópodos que pesca el Japón, la falta de conocimientos sobre la relación población/reclutamiento y la gran fluctuación de las poblaciones capturables que se registra cada año han hecho difícil la utilización de modelos analíticos para evaluar las poblaciones. Por consiguiente, los estudios sobre esas poblaciones se han ocupado principalmente del cálculo de biomasa utilizando el método de expansión zonal, que es el mejor medio de que se dispone por el momento para estimar el tamaño y el rendimiento potencial de una población. Los resultados obtenidos indican que aún no se ha explotado al máximo la pesca de las tres especies de calamares mencionadas, aunque la gran variación de reclutamiento anual hace difícil determinar un nivel fijo de rendimiento constante para esas especies de poca vida.

1. THE HISTORICAL PROGRESS OF JAPANESE DISTANT-WATER FISHERIES FOR CEPHALOPODS

The current Japanese distant-water fisheries for cephalopods cover a significant part of the world's oceans; extending over the coastal and offshore waters of seven major fishing areas, namely the Eastern Central Atlantic, Southeast Atlantic, Northwest Atlantic, Southwest Atlantic, Northeast Pacific, Southwest Pacific and the Northwest Indian Ocean. The main commercial catches are composed of around 14 species including squid, cuttlefishes and octopuses (Table 1).

The first full-scale cephalopod fisheries by Japanese trawlers in distant waters began off the coasts of Spanish Sahara and Mauritania in the Eastern Central Atlantic in the mid-sixties, where the most active fisheries for cuttlefishes, *Sepia officinalis* and *S. bertheloti*, and octopus, *Octopus vulgaris*, were carried out toward the mid-seventies. Thereafter, the cuttlefish fishery fell into decay due to the loss of the former main fishing grounds off the Spanish Sahara and only the octopus fishery has been continued, mainly in Mauritanian waters under the Japan/Mauritania fishery agreement.

Japanese trawlers began another cuttlefish fishery in the Arabian Sea in 1967. They operated in the coastal waters extending from Oman to Somalia until 1973, and thereafter concentrated on the waters off the coast of the P.D.R. of Yemen, where the most promising fishing grounds for cuttlefish, *Sepia pharaonis*, were exploited. Since then cuttlefish off Yemen has become one of the most important alternate target species for the Japanese cephalopod fishery in place of African cuttlefish.

In the Northwest Atlantic, Japanese trawlers began taking long-finned squid, *Loligo pealei*, on and along the continental edges off the northeast coast of America early in the seventies. This directed fishery was continued until 1975; the fleet switching regularly from butterfish to squid, and vice versa. However, the strengthening of regulations on foreign fisheries in American waters in 1976 caused the Japanese squid fishery to change the target species to short-finned squid, *Illex illecebrosus*, in Canadian waters. Since then the *Illex* fishery by Japanese trawlers has been continued on and along the edges of the Scotian Shelf south of Nova Scotia under the Japan/Canada fishery agreement, as one of the most important Japanese cephalopod fisheries. In addition to trawling, some Japanese squid-jigging vessels began operating in the southern Canadian waters under the Japan/Canada cooperative fishery in 1978.

Table 1

Commercially important species of cephalopods exploited by Japanese distant-water fisheries

Family	Species	Area (Fishing grounds)	Gears used[a]
Sepiidae	*Sepia officinalis* LINNAEUS	Eastern Central Atlantic (N.W.African coastal)	TR
	S. btheloti D'ORBIGNY	Eastern Central Atlantic (N.W.African coastal)	TR
	s. pharaonis EHRENBERG	West Indian Ocean (Arabian Sea: P.D.R.Yemen coastal)	TR
Loliginidae	*Loligo forbesi* STEENSTRUP	Eastern Central Atlantic (N.W.African coastal)	TR
	L. vulgaris LAMARCK	Eastern Central Atlantic (N.W.African coastal)	TR
	L. pealei LESUEUR	Northwest Atlantic (American coastal)	TR
	L. reynaudi D'ORBIGNY	Southeast Atlantic (S.African coastal)	TR
Gonatidae	*Berryteuthis magister* (BERRY)	Northeast Pacific and Bering Sea	TR
Ommastrephidae	*Illex illecebrosus* (LESUEUR)	Northwest Atlantic (Canadian and American coastal)	TR, SJ
	I. argentinus (CASTELLANOS)	Southwest Atlantic (Argentine coastal)	TR
	Nototodarus sloani GRAY	Southwest Pacific (New Zealand waters)	TR, SJ
	N. s. gouldi (MCCOY)	Southwest Pacific (Tasman Sea: S.E.Australian coastal)	SJ
Octopodidae	*Octopus vulgaris* LAMARCK	Eastern Central Atlantic (N.W.African coastal)	TR
	O. dofleini apollyon (BERRY)	Northeast Pacific and Bering Sea	TR

[a] TR : otter trawl (mostly bottom trawl), SJ : squid-jigger

In the southwest Pacific, Japan started a directed fishery for arrow squid, *Nototodarus sloani*, in New Zealand waters early in the seventies. Japanese squid-jigging vessels first exploited some promising fishing grounds off the west coast of North Island and the east coast of South Island, and then embarked on a full-scale operation in 1973. Following that, Japanese trawlers began a directed fishery for arrow squid on the traditional fishing grounds, and for other target species off the east coast of South Island. After the enforcement of the 200-mi Exclusive Economic Zone by New Zealand, the Japanese trawl fishery extended the scope of its operations to offshore plateau areas to cover the loss of traditional coastal fishing grounds, and subsequently exploited some good fishing grounds for arrow squid on the waters of the plateau south of South Island. A full-scale squid fishery in offshore waters inside the 200-mi limit thus began in 1979, and since then the newly exploited stock has been one of the most important targets for the Japanese trawl fishery in New Zealand waters. The squid-jigging fishery has continued centring around the traditional fishing grounds, but recently some squid jiggers shifted to Australian waters due to the restriction in the number of licensed vessels in New Zealand waters and began taking another kind of squid, *Nototodarus sloani gouldi*, mainly in the western Tasman Sea on an experimental basis.

To meet an increasing domestic demand for Loliginid squid, in 1974 Japan began a directed fishery for long-finned squid, *Loligo reynaudi*, on the banks off the south coast of South Africa, and since then this squid has become one of the most important target species for the Japanese trawl fishery in the Southeast Atlantic.

In the northern Pacific, extending from the Bering Sea to the northeast Pacific, Japanese trawlers began taking gonatid squid, *Berryteuthis magister*, late in the seventies. The exact extent of the fishing grounds has not been fully established yet, but this species is worth considering for further exploitation.

In the southwest Atlantic, Japanese trawlers discovered the existence of a large population of short-finned squid, *Illex argentinus*, in Argentine waters south of 40°S, and began a directed fishery in 1978 on an experimental basis. However, they shifted to waters outside the 200-mi limit in the next year due to the strengthening of restrictions on foreign fisheries by Argentina, and have been operating a directed squid fishery there since then.

The annual catches of cephalopods by Japanese distant-water fisheries in each of the traditional and recently exploited fishing grounds for the years 1967-80, are summarized in Table 2. The aforementioned historical progression of Japanese overseas fisheries for cephalopods is well reflected in the annual changes in cephalopod catch from each fishing area in Table 2. The noticeable decreases in the catch of coastal cephalopods (*Loligo* squid, cuttlefish and octopus) observed in many of the traditional fishing grounds in and after 1975 (Table 2) were mainly caused by the inevitable reduction of foreign fishing operations in those waters resulting from the increase of restrictions imposed on distant-water fisheries by the coastal countries concerned.

Table 2 shows also that Japanese distant-water fisheries for cephalopods in recent years have strongly depended upon ommastrephid squid in both Canadian and New Zealand waters, and on octopus in Mauritanian waters. However, in consequence of the progress in efficiency of operation and directed exploitation of available stocks, annual total catches of cephalopods by Japan in recent years have been well maintained at the same level of approximately 70 000-110 000 t as before 1975, when most of Japanese cephalopod fisheries could operate rather freely.

Under such a situation, the catch of oceanic squid (ommastrephid and gonatid squid), which remained at about 3 600 t/year at most, up until 1972, has sharply increased thereafter and reached approximately 80 000-81 000 t/year, accounting for 71-87 percent of the annual total cephalopod catches under consideration, in and after 1978. This sharp increase in the catch of oceanic squid in the last three years under the newly established 200-mi limit was the direct outcome of all possible efforts made by Japanese overseas fisheries to exploit available stocks in offshore waters including the open sea, instead of the stocks forfeited on the traditional inshore fishing grounds, in order to meet an increasing domestic demand for squid.

Table 2

Historical catch of cephalopods by Japanese distant-water fisheries, 1967–80[a]

(in tons)

Fishing Area	Species	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980
Northeast Pacific and Bering Sea	Berryteuthis magister[b]	+	+	+	+	+	+	+	+	+	+	7056	9023	5305	5302
	Octopus dofleini apollyon[b]	+	+	+	+	+	+	+	+	+	+	1222	192	539	291
	TOTAL	+	+	+	+	+	+	+	+	+	+	8278	9215	5844	5593
Southwest Pacific (New Zealand and Australia)	Nototodarus sloani	-	-	204	353	46	728	19121	21583	20846	25521	47143	35554	25385	50001
	Nototodarus sloani gouldi	-	-	-	-	-	-	-	-	-	-	21	56	488	8514
	TOTAL	-	-	204	353	46	728	19121	21583	20846	25521	47164	35610	25873	58515
West Indian Ocean (Arabian Sea)	Sepia pharaonis[b]	+	+	4530	3427	5333	8054	5009	5907	4156	10291	9476	3325	6235	3859
Eastern Central Atlantic (Northwest Africa)	Sepia spp.	31672	29374	24054	12325	15914	21446	21196	11670	7303	2371	2395	3739	4158	1937
	Loligo spp.	11524	6650	5617	4310	5102	4649	4441	5965	1152	389	472	343	170	6[c]
	Octopus vulgaris	53837	72914	46154	39744	38063	33003	29834	28145	24526	24636	26096	19818	9633	15[c]
	TOTAL	97063	108961	75986	56453	59155	59549	55952	45997	33172	27501	28989	23920	13969	1960
Northwest Atlantic (America and/or Canada)	Loligo pealei	4	178	7123	13244	11435	15870	14471	13375	11231	5169	7833	2657	3175	6016
	Illex illecebrosus	2	1653	584	454	209	2402	1150	3671	4371	6527	7771	29519	33834	18997
	TOTAL	6	1830	7707	13698	11644	18271	15621	17047	15603	11696	15604	32176	37009	25012
Northeast Atlantic	Loligo forbesi	-	-	35	-	44	93	177	67	-	-	-	-	-	-
Southwest Atlantic (Argentina)	Illex argentinus	-	-	-	-	-	-	-	-	-	-	0	6920	14903	6148
TOTAL AREA	Sepia spp.	31682	29353	28585	14185	21247	29500	26043	17213	11352	11906	11586	6893	10116	5592
	Loligo spp.	11563	6866	12927	17831	16689	20868	19593	21923	15231	6858	10504	6381	5863	7211
	Ommastrephidae & Gonatidae	32	1680	950	773	332	3640	20907	26148	25566	32812	62254	80950	80130	89203
	Octopus spp.	53481	72914	46154	39744	38063	33003	29834	28145	24534	24644	27322	20010	10172	308
	TOTAL	97117	110813	88616	72534	76331	87010	96377	93429	76683	76219	111666	114234	106280	102313

[a] Data from the Far Seas Fisheries Research Laboratory and the Hokkaido Regional Fisheries Research Laboratory

[b] Includes some other species but negligible

[c] The directed octopus fishery was suspended due to the failure of the agreement on fisheries between Japan and Mauritania

+ No statistics on cephalopod catch are available

2. ASSESSMENTS OF SEVERAL CEPHALOPOD STOCKS TARGETED BY JAPANESE FISHERIES

2.1 Stock Assessment of Common Octopus, *Octopus vulgaris*, off the Coast of Northwestern Africa

A single species of octopus, *Octopus vulgaris*, has been reported from the commercial catches in the waters off the coast of northwestern Africa.

The Japanese trawl fishery began operating in these waters late in the fifties. In the very early stage of the fishery, up until the beginning of the sixties, it aimed mainly at seabreams and cuttlefishes rather than octopus, but the discovery of large stocks of octopus off the coasts of Spanish Sahara and Mauritania in the mid-sixties led to a successful development of the octopus-directed fishery by Japanese trawlers. A full-scale Japanese octopus fishery in these waters thus began in 1965, and since then common octopus has become one of the most important target species for the Japanese distant-water trawl fishery.

Annual catches (total by countries) of octopus off the coast of northwest Africa (9°N-36°N) for the years 1967-79 are shown in Table 3. The annual total catch of octopus had remained at a level of about 100 000 t up until 1978, but declined sharply to around 60 000 t in 1979 mainly due to the closure of the territorial waters of Mauritania to foreign octopus fisheries. The majority of the annual total catch was divided between Japan and Spain until 1970, but Spanish catches exceeded Japanese ones thereafter, and since accounted for over 60 percent of the total in most years. On the other hand, contrary to the gradual decreases in Japanese catch, the Korean catch has sharply increased since 1974. Subsequently, the USSR and Morocco have been among those countries fishing substantial quantitites of octopus since 1977 and 1978, respectively; their combined catch in 1978 accounted for about 12 percent of the annual total catch slightly exceeding the Korean catch.

Three main fishing grounds for octopus are found off the coasts of former Spanish Sahara and Mauritania, and Japanese fishermen distinguish them by the name of Villa Cisneros, Cap Blanc and Nouakchott regions, respectively (Figure 1). These grounds are well separated from each other, and it is assumed that the octopus on each fishing ground forms an independent local stock.

Since the middle of the sixties, the Villa Cisneros and Cap Blanc regions have been the most important fishing grounds for Spanish and Japanese octopus fisheries, respectively. On the other hand, the Nouakchott region has been exploited mainly by Japanese trawlers since around 1969, but the stock size of octopus seems to be very small compared to those in the above two regions.

The status of octopus stocks in the northern part of the CECAF area (Fisheries Commission for the Eastern Central Atlantic) was assessed in a preliminary way at the Second Session of the CECAF Working Party on Resource Evaluation by applying firstly the general production model to the overall stock in the area (CECAF, 1975). In the analysis, Japanese CPUE for the Sahara Coastal Division was related to the total uncorrected fishing effort (total reported catch/Japanese CPUE). However, the result of the analysis was difficult to interpret in terms of estimating the maximum potential. The resultant equilibrium yield curve and MSY (maximum sustainable yield) value were obviously too low, since the total catch did not include the unreported catches from some countries fishing substantial quantities of octopus and also the Japanese CPUE index applies for only part of the area, and would not always be representative of that for the whole stock in the area.

The CECAF *Ad Hoc* Working Party on the Assessment of Cephalopod Stocks (CECAF, 1978) was able to assemble more detailed annual total catches of octopus by divisions north of Cape Verde for the years 1966-77, and these correspond to series of CPUE data based on Japanese and Spanish statistics, although the total catches are still only partially complete due to the lack of catches from some countries fishing substantial quantities of octopus. The Japanese and Spanish CPUEs could be referred to specific fishing grounds to a large extent, but no separate catch statistics for each fishing ground, covering the whole period of exploitation, were available. Therefore, only an overall assessment of octopus stocks in the northern zone of CECAF (corresponding essentially to the Villa Cisneros, Cap Blanc and Nouakchott stocks) could be made.

Table 3

Nominal catches of common octopus, *Octopus vulgaris*, by countries off the coast of Northwest Africa (9°N-36°N)[a]

(in tons)

Country	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979
Argentina	900	400	-	400	600	499	400	-	-	0	0	-	-
Bulgaria	-	-	-	62	42	-	-	-	-	-	-	-	-
Greece	1060	1394	2767	688	1073	749	880	707	175	112	75	137	210
Italy	3461	3168	3372	1456	1875	2190	1033	2567	-	-	457	351	10
Japan[b]	53837	72914	46154	39744	41422	33003	29834	28145	24526	24636	26096	19818	9633
Korea	-	-	1154	2134	1773	1230	3708	6650	10525	19190	10113	11079	7502
Mauritania	187	217	260	440	440	814	120	-	100	100	100	100	100
Morocco	-	-	-	-	-	-	-	-	-	-	-	6004	3877
Portugal	-	-	-	-	-	-	-	28	24	34	-	5	1
Romania	-	-	-	-	-	-	-	5	34	-	1	-	-
Spain	41127	41303	37768	30119	67283	87267	46400	85267	92621	71654	51480	53719	40447
Taiwan	-	-	-	-	-	-	-	-	-	-	-	1038	39
USSR	-	-	-	-	-	-	-	-	-	-	7811	6037	56
TOTAL	100572	119396	91475	75043	114508	125752	82375	123369	128005	115726	96113	98288	61875

[a] Catches by countries other than Japan were cited from the following statistics:
(i) CECAF Statistical Bulletin, No. 2 (FAO, 1979)
(ii) Report of the Fifth Session of CECAF WP on Resources Evaluation (CECAF, 1981)
(iii) Yearbook of Fisheries Statistics, Vol. 48 (FAO, 1980)

[b] Data from the Far Seas Fisheries Research Laboratory, Japan Fisheries Agency

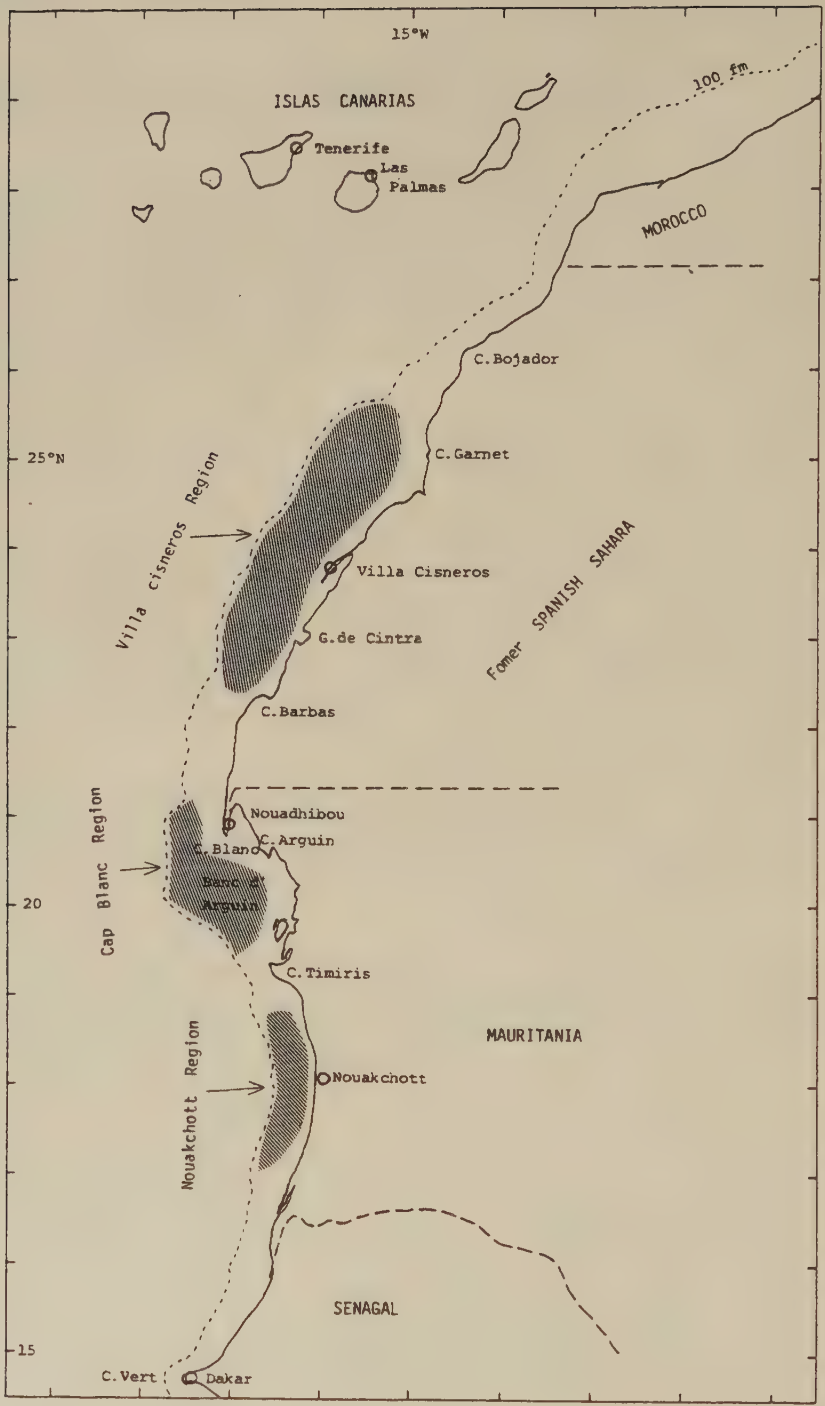

15°W
ISLAS CANARIAS
Tenerife
Las Palmas
100 fm
MOROCCO
C.Bojador
25°N
C.Garnet
Villa cisneros Region
Villa Cisneros
Fomer SPANISH SAHARA
G.de Cintra
C.Barbas
Nouadhibou
C.Blanc
C.Arguin
Cap Blanc Region
Banc d' Arguin
20
C.Timiris
MAURITANIA
Nouakchott Region
Nouakchott
SENAGAL
15
C.Vert
Dakar

Figure 1 Fishing grounds for octopus, *Octopus vulgaris* off the northwest coast of Africa

For the production model, the series of Japanese and Spanish CPUEs were combined; weighting for their respective catches. The logarithm of the CPUE was then regressed on the standardized effort in the same year using a functional regression to fit the curve to the annual points, including the observed value for 1977. The estimates given for the MSY and SY (sustainable yield at $F_{0.1}$ were about 109 000 t with an effort of 830 000 h and 107 000 t with an effort of 670 000 h, respectively, and this led to the conclusion that the total effort deployed in 1977 was 30 percent higher than that corresponding to the MSY.

Hatanaka (1979) made a detailed stock assessment of the octopus in the Cap Blanc region on the basis of Japanese catch and effort data, total catches from the ground for the years 1967-75, and various biological and stock parameters estimated.

Firstly, applying the areal expansion method, the stock size in number by year classes was calculated from Japanese catch rates (catch in number per hour fished) by depth strata for the years 1967-71, when the majority of total annual catches of octopus from the ground (about 88 percent on average) were taken by Japanese trawlers. Based on the results, total annual mortality (Z) exclusive of the loss of spawners after breeding was estimated to be about 1.2 for the years 1967-75 with due regard to the seasonal and annual changes in vulnerability, as well as the stability of fishing effort during the period.

Secondly, the Beverton-Holt yield per recruit equation (dynamic pool model) was applied to the stock on the basis of the mortality estimates and the biological parameters. The age at first capture in recent years was assumed to be 1.2 years on average. The yield per recruit curve suggested that the yield of Cap Blanc octopus can be slightly increased, since the isopleth diagram of yield per recruit showed that if first capture is shifted from 1.2 to 1.6 years of age (from about 63 cm to 76 cm in total length) and the fishing effort is increased by 30 percent over that exerted in recent years, the yield per recruit should increase 10 percent over the recent level[1/].

Finally, the potential yield was estimated by applying the Schaefer production model to the stock. The Japanese CPUE was related to the mean standardized effort for each two years running, and the regression line was given by the equation:

$$\mathrm{CPUE} = 523 - 0.0024\bar{f}$$

where CPUE = kg/h fished

$\bar{f}$ = mean fishing effort in 1 000 h for 2 years running

The correlation coefficient was −0.78. The resultant parabolic equilibrium yield curve showed that the MSY was at about 28 000 t with an effort of 108 000 h fished. From this it was concluded that the fishery had been operating at around the optimum level since about 1970, and that urgent introduction of any additional regulations would not be necessary for the protection of the octopus stock in the Cap Blanc region.

For the octopus stock in the Villa Cisneros region where the traditional Spanish directed fishery for octopus has operated, the data available were not sufficient for an assessment. However, it was noticed that the Japanese CPUE for octopus had dropped sharply since 1971, and the size of octopus at first capture was considerably smaller than in the Cap Blanc region, and it was stressed that the preparation of detailed catch and effort data, as well as full CPUE information available for octopus, was essential for a reasonable assessment. In this context, it was also recommended that the introduction of some reasonable regulations on the fishery should be discussed as soon as possible.

[1/] Editor's note: Such a small predicted increase is however likely to be well within the range of error in estimating the biological parameters, and therefore, probably is not significant

Subsequently, Pereiro and Bravo de Laguna (1980) assessed the state of octopus stock in and around the Villa Cisneros region based on the Spanish catch and effort data for the years 1964-79. For this analysis, the Beverton-Holt yield per recruit equation and the general production model were applied to the stocks. Although the catch and effort statistics by fishing grounds were unavailable and hence the separation of local stocks was insufficient, the results obtained were substantially the same as those achieved by Hatanaka (1979).

The most recent stock assessment of octopus was made at the Fifth Session of the CECAF Working Party on Resource Evaluation in 1980 (CECAF, 1981). The Working Party assessed the state of each of the Cap Blanc and Villa Cisneros stocks, separately. For the Nouakchott stock, the data available were insufficient for an assessment.

The Cap Blanc Stock

Only the Japanese catch and effort data and corresponding CPUEs for the years 1967-79 were known; catches of other countries were arbitrarily estimated according to general information on the periodical changes in their participation in the fishery in this area. The resultant figures are shown in Table 4.

The general production model (Pella and Tomlinson, 1969) was applied to the stock, which is based on the relationship:

$$u = (a + bf)^{\frac{1}{m-1}} \quad \text{and} \quad Y = f(a + bf)^{\frac{1}{m-1}}$$

where u = catch per unit of effort
f = fishing effort
Y = catch
a, b and m are coefficients defining the inherent potential for population growth

The best statistical adjustment was obtained when $m = 0.50$ by adopting an iterative procedure to minimize the difference between the observed and predicted catches in each year. The resultant equilibrium yield curve gave an MSY of about 38 300 t with an effort of 126 000 h. Assuming this analysis was correct, the Working Party concluded that the stock appeared to be exploited at a level inferior to the MSY, with recent effort inferior to the f_{MSY} level.

The Villa Cisneros Stock

Catches were estimated by taking the difference between the total octopus catch for the northern sector of CECAF and the estimated catch for the Cap Blanc stock (Table 5).

The best adjustment of the general production model was obtained when $m = 0.24$ and the result gave an MSY of about 70 000 t with an effort of 382 000 h. The Working Party considered therefore that this stock is being exploited with an effort much higher than that at the optimum level, and is being greatly overexploited.

Cohort analysis was applied experimentally to the Cap Blanc stock using data on Japanese monthly catch in number by age groups estimated by Hatanaka (1979) for the years 1967-71. Independent analyses were made on males and females by retaining a constant natural mortality of 0.5 as the agreed assumption and the results suggested that a recruitment to the fishery of between 25 million and 50 million individuals at 7 months of age was a reasonable hypothesis. The average fishing mortalities (from 7 to 36 months old) based on the hypothesis of 25 million recruiting annually, were 0.61 and 0.31 for males and females, respectively, and on the hypothesis of 50 million recruiting fisheries were 0.20 and 0.14, respectively.

Ricker's yield per recruit model was also applied to the data. For either males or females, it appeared that the stock was heavily exploited and was only moderately exploited in terms of yield per recruit for the recruitments of 25 million and 50 million, respectively. Taking into account that the Cap Blanc stock seemed to be fully exploited, the Working Party considered that a possible annual recruitment at the 25 million level was the most likely hypothesis, at least in terms of production model at the early stage of exploitation, though the relationship between the yield per recruit and the stock production curve cannot be compared directly.

Table 4

Original data on octopus catch, effort and CPUE in the Cap Blanc region for the estimation of the equilibrium yield[a]

Year	Catch in tons			CPUE[b] (kg/hour)	Effort (hours)
	Japan	Other countries	Total		
1967	23 422	-	23 422	691	33 896
1968	25 615	-	25 615	599	42 763
1969	54 751	-	54 751	693	79 006
1970	24 479	3 599[c]	28 078	454	61 846
1971	35 946	7 374[c]	43 320	324	133 704
1972	32 433	9 246[c]	41 679	313	133 160
1973	24 080	4 624[c]	28 704	327	87 780
1974	23 446	6 937[c]	30 383	258	117 764
1975	26 371	13 288[d]	39 659	203	195 365
1976	15 825	18 161[d]	33 986	170	199 918
1977	26 435	13 513[d]	39 948	225	177 547
1978	24 603	13 036[d]	37 639	360	104 553
1979	18 338	8 759[d]	27 097	210	129 033

a/ Data from the report of the 5th session of the CECAF Working Party on Resources Evaluation (FAO, 1980; CECAF, 1981)
b/ Catch rate by Japanese standard trawlers (550-1000 GRT)
c/ 10 % of the catches from the northern sector of Cape Verde
d/ 20 % of the catches from the northern sector of Cape Verde

Table 5

Original data on octopus catch, effort and CPUE in the Villa Cisneros region for the estimation of the equilibrium yield[a].

Year	Catch in tons			CPUE[b] (kg/hour)	Effort (hours)
	Japan	Other countries	Total[c]		
1967	23 674	76 430	100 104	347	220 986
1968	23 455	97 529	120 984	416	229 252
1969	14 751	78 693	93 444	313	123 620
1970	4 725	72 525	77 250	185	265 795
1971	3 660	110 050	113 710	170	414 059
1972	4 735	122 925	127 660	126	682 246
1973	3 001	81 897	84 898	103	545 573
1974	1 660	101 711	103 371	63	1,158 540
1975	392	96 069	96 461	50	1,136 140
1976	244	117 821	118 065	59	1,425 068
1977	24	101 222	101 246	39	1,571 744
1978	15	90 217	90 232	43	1,223 093
1979	4	59 564	59 568	27	1,202 630

a/ Data from the same report with Table 3.
b/ Average of the Spanish and Japanese CPUEs
c/ Difference between total octopus catch for the northern sector of Cape Verde and estimated catch for the Cap Blanc stock

Recently, Hatanaka made a tentative calculation of the MSY and the optimum effort for the octopus stock in each of the Cap Blanc and Villa Cisneros regions on the basis of the revised estimates of catch and effort for the years 1967-79 and corresponding Japanese and Spanish CPUEs. No separate catch and effort statistics by regions on other foreign fisheries being available, annual reported catches by other countries for the northern sector of Cape Verde were allocated to either of the two regions according to reliable information on foreign fisheries obtained from Japanese fishing companies concerned. The resultant estimates for each stock are shown in Table 6.

By fitting the Gulland-Fox production model to the CPUE and effort data available, the MSYs were evaluated to be about 44 000 t with an effort of 185 000 h, and 70 800 t with an effort of 683 000 h for the Cap Blanc and Villa Cisneros stocks, respectively (Figure 2). The results obtained are quite similar to the estimates by the CECAF Working Party in 1980, which suggest that the fishery for Cap Blanc octopus has been operating below the f_{MSY} level since 1978 and that the Villa Cisneros stock has been greatly over-exploited in recent years.

2.2 Stock Assessment of a Long-Finned Squid, *Loligo reynaudi*, on the Agulhas Bank off the South Coast of South Africa

The range of geographical distribution of the chokker squid, *Loligo reynaudi*, is not well understood at present.

In the ICSEAF (International Commission for the Southeast Atlantic Fisheries) area, these squid are caught by bottom or off-bottom trawlers. Catches have been reported from fishing grounds shallower than 200 m on the middle and western parts of the Agulhas Bank off the south coast of South Africa, extending from the south of Cape Town to the south of Port Elizabeth (Figure 3).

The squid under exploitation are assumed to be composed of a single stock. This stock has been eagerly exploited by Japan since around 1974 to meet an increasing domestic demand for loliginid squid. The further exploitation of new populations and/or new stocks of this species on the Agulhas Bank, east of Port Elizabeth, seems quite possible.

Catches (total, and by countries) of this species for the years 1971-80 are shown in Table 7. Almost all of the catches have been taken by Japan and South Africa. Both national catches increased sharply in and after 1974, due to the beginning of directed fisheries for this species, and total annual catches have remained at approximately 2 000-5 000 t since then. The majority of Japanese catches have been taken at a depth of between 60 m and 140 m on the middle part (20°E-25°E) of Agulhas Bank, where this squid is more abundant than on all other exploited grounds outside territorial waters.

The directed squid fishery by Japan has operated intermittently every year since around 1975, but most Japanese squid catches have been taken as a by-catch to the jack mackerel fishery. The main fishing seasons for squid are usually in summer (from November up to around February of the next year) and early in winter in the southern hemisphere, centred around June. However, sometimes either or none of the said main fishing seasons are observed and sometimes better catches occur in different seasons.

Two series of monthly CPUE figures for chokker squid by Japanese standard trawlers (2 500-3 000 GRT) are shown in Table 8. Some considerable year-to-year fluctuations are recognizable among the monthly changes in the mean squid CPUE by Japanese fisheries directed to other target species. Insufficient data on the monthly CPUE by the Japanese directed squid fishery are available for comparison, but both show a higher value than the corresponding monthly CPUE for squid taken in other fisheries. In neither case is there a definite increasing or decreasing tendency in the annual changes in CPUE during the period 1975-80. This might suggest the existence of a sustainable level of harvesting in spite of the occurrence of year-to-year fluctuations in the recruitment to the present fishing grounds.

However, the catch and effort data available, as well as the knowledge of biological characteristics are too poor to further advance the stock assessment studies of this species for the time being. Under these circumstances, the direct estimation of standing

Table 6

Estimated catches (t) and catch rates (kg/h fished) of *Octopus vulgaris* and fishing efforts (h fished) by trawlers by fishing grounds off the coast of northwest Africa[a]

Fishing grounds		Country	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979
Cap Blanc	Catch	Japan	30112	49346	31029	33467	32440	26145	24887	23117	21400	23251	25060	18754	9552
		Korea[b]	-	-	-	-	-	-	-	-	6315	11514	6068	6647	4501
		Mauritania[c]	187	217	260	440	440	814	120	-	100	100	100	100	100
		Spain[d]	4113	4130	3777	3012	6728	8727	3861	16545	17943	14323	10288	10738	7943
		USSR[e]	-	-	-	-	-	-	-	-	-	-	3906	3019	28
		Total	34412	53693	35066	36919	39608	35686	28868	39662	45758	49188	45422	39258	22124
	Catch rate	Japan[g]	583	569	350	363	318	263	225	195	172	195	287	250	-
	Effort	Total[i]	59026	94364	100189	101705	124553	135688	128302	203395	266035	252246	158265	157032	-
Villa Cisneros	Catch	Bulgaria[f]	-	-	-	62	42	-	-	-	-	-	-	-	-
		Japan	23674	23455	14751	4725	3660	4735	3001	1660	392	244	24	15	4
		Korea[b]	-	-	1154	2134	1773	1230	3708	6650	4210	7676	4045	4432	3001
		Morocco[f]	-	-	-	-	-	-	-	-	-	-	-	6004	3877
		Portugal[f]	-	-	-	-	-	-	-	28	24	34	-	5	1
		Romania[f]	-	-	-	-	-	-	-	5	34	-	1	-	-
		Spain[d]	37014	37173	33991	27107	60555	78540	34750	66181	71772	57293	41154	42942	31774
		Total	60688	60628	49896	34028	66030	84505	41459	74524	76432	65247	45224	53398	38657
	Catch rate	Spain[h]	-	-	244	210	212	120	95	74	55	59	39	43	27
	Effort	Total[i]	-	-	204492	162038	311462	704208	436411	1007081	1389673	1105881	1159590	1241814	1431741

[a] Based on the same catch data with Table 3

[b] Estimated that the catch was taken in Villa Cisneros waters before 1974 every year and that 60 % and 40 % of the annual catches were taken in Cap Blanc and Villa Cisneros waters, respectively, in and after 1975

[c] Estimated that all of the catches were taken in Cap Blanc waters

[d] Estimated that 10 % and 20 % of the annual catches from CECAF Division 1.3 were taken in Cap Blanc waters before 1973 and from 1974 onward, respectively

[e] Estimated that 50 % of the annual catches were taken from Cap Blanc waters

[f] Estimated that all of the catches were taken in Villa cisneros waters

[g] Catch rate (Kg/hour fished) for the standard trawlers belonging to 550-1000 tonnage class

[h] Cited from b) shown in Table 3

[i] Total catch/Catch rate ; in hours fished

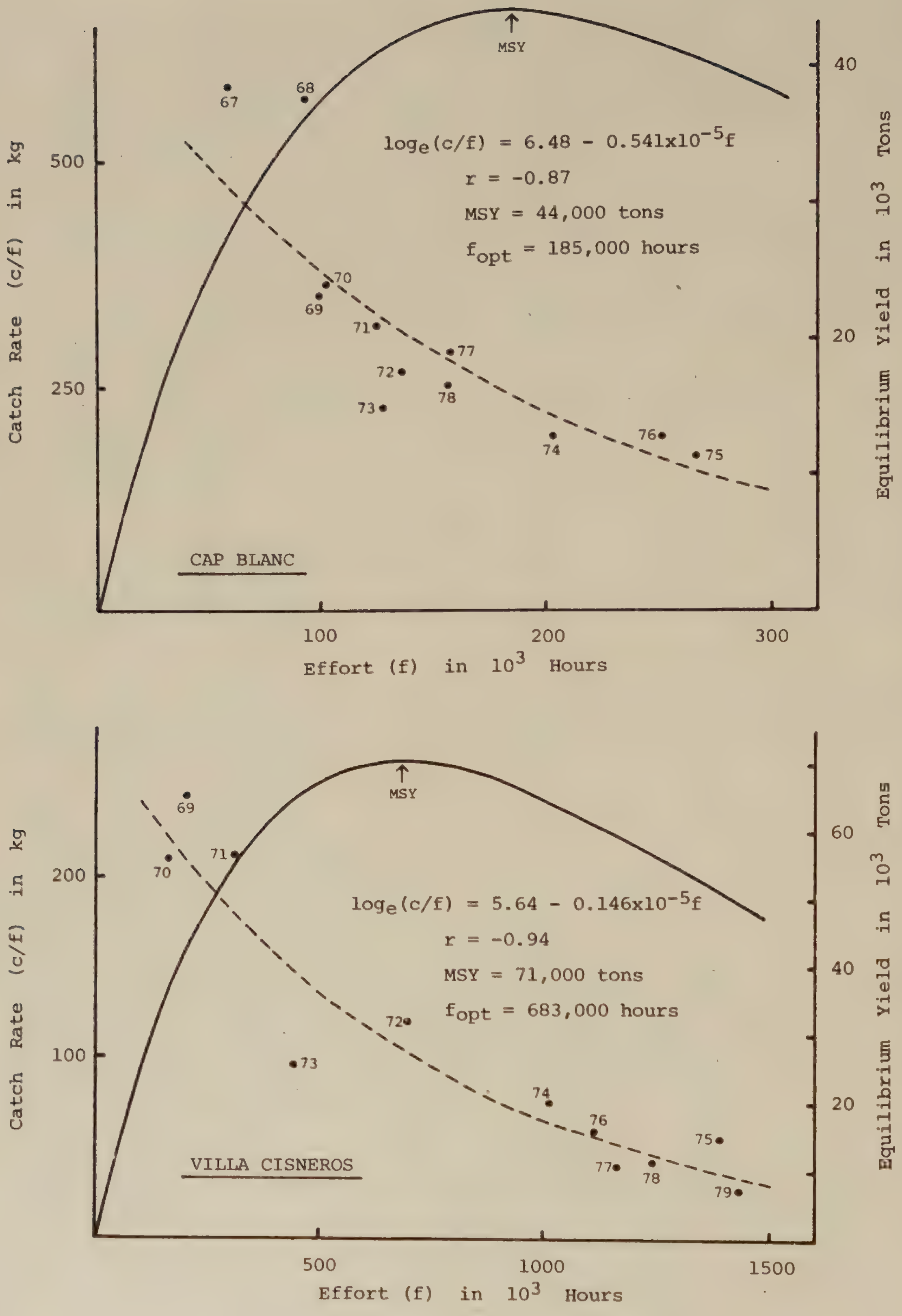


Figure 2 Relationship between catch rate and corresponding fishing effort, and equilibrium yield curve for octopus, *Octopus vulgaris*, in each of Cap Blanc region (upper) and Villa Cisneros region (lower)

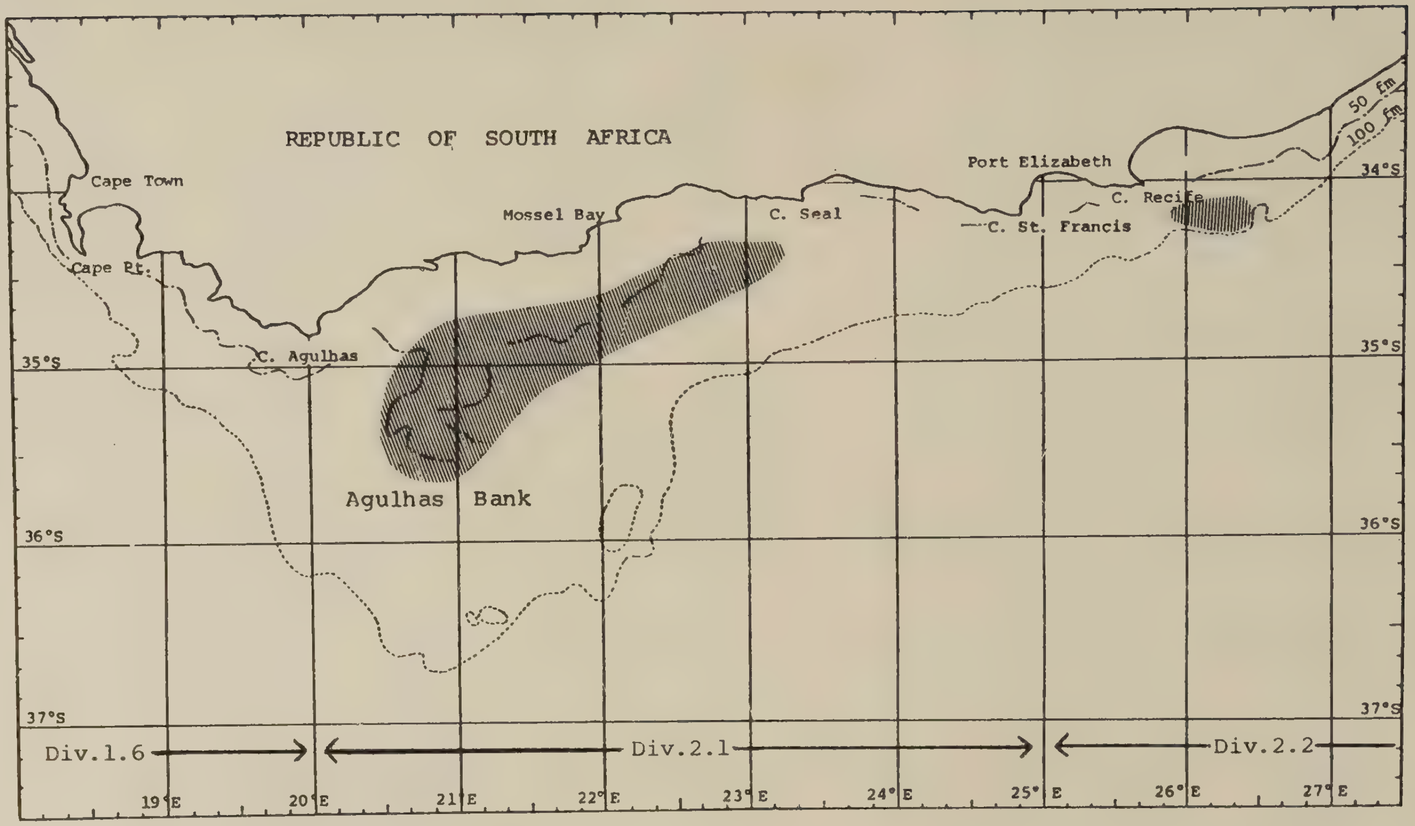

REPUBLIC OF SOUTH AFRICA
Cape Town
Cape Pt.
C. Agulhas
Mossel Bay
C. Seal
Port Elizabeth
C. St. Francis
C. Recife
50 fm
100 fm
Agulhas Bank
34°S
35°S
36°S
37°S
19°E
20°E
21°E
22°E
23°E
24°E
25°E
26°E
27°E
Div.1.6
Div.2.1
Div.2.2

Figure 3 Chart showing the Agulhas Bank area and the localities of Japanese main fishing grounds (shadowed area) for long-finned squid, *Loligo reynaudi*. ICSEAF Statistical Divisions are also shown in the figure, namely: Division 1.6 = Cape of Good Hope, Division 2.1 = Middle Agulhas, Division 2.2 = Eastern Agulhas

Table 7

Nominal catches of long-finned squid, *Loligo reynaudi*, by countries on the Agulhas Bank off the south coast of South Africa

(tons)

Country	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980
Japan[a/]	73	218	366	2304	2810	1089	2134	3004	2419	1149
South Africa[b/]	+	294	571	(1318)	(839)	(1018)	(1148)	(1986)	(2574)	+
Others[b/]	-	-	-	-	-	2	20	-	-	+
Total	73	512	937	(3622)	(3649)	(2109)	(3302)	(4990)	(4993)	+

a/ Data from the Far Seas Fisheries Research Laboratory, Japan Fish. Agency

b/ Cited from ICSEAF Statistical Bulletins, No.1 - No.9

( ), denoting the combined catch of Loliginid and Ommastrephid squids, but most of them seem to be Loligo reynaudi

+ , no statistics are available

Table 8

CPUE (kg/h) of long-finned squid, *Loligo reynaudi*, by Japanese standard trawlers (2 500-3 000 GRT) in ICSEAF subarea 2

Fishery	Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Ann. mean
Squid direct fishery	1975	-	-	-	-	-	701	-	-	-	-	53	560	475
	1976	-	-	-	-	-	-	-	-	-	-	-	250	250
	1977	558	375	379	-	-	775	255	-	-	-	44	-	493
	1978	-	-	-	-	-	431	-	-	-	275	368	256	308
	1979	340	248	-	206	-	-	-	-	372	-	-	-	307
	1980	-	-	-	-	-	-	-	-	-	271	-	-	271
Direct fisheries for other species	1975	25	28	30	11	7	6	5	20	21	10	35	33	19
	1976	17	13	12	26	31	15	7	12	28	27	36	114	30
	1977	418	108	15	7	7	91	20	16	26	66	38	11	59
	1978	18	22	13	38	19	23	10	13	8	139	291	69	63
	1979	62	31	47	85	15	2	5	31	94	85	140	114	56
	1980	8	29	11	21	8	9	9	16	33	97	132	103	42

stock size will be the only possible way to overcome the impasse. In this context, a Japan/South Africa joint trawling survey was carried out on the Agulhas Bank from November to December 1980, using a Japanese commercial trawler, and the stock size of the squid at that time of the year was estimated by applying the areal expansion method.

The survey was performed on the Agulhas Bank shallower than 100 fathoms (excluding South African territorial waters within 12 n mi), between 18°30'E and 27°00'E, and covering approximately 20 500 n mi². The trawl stations were selected by the stratified random sampling method. The survey area was divided into 1 003 units of 5'-square blocks and these blocks were stratified into 12 strata by the 50 and 100 fathoms depth contours and longitudinal lines on a block-to-block basis (Figure 4).

A total of 218 trawlings, 145 in the daytime and 73 at night, were carried out at different stations using a regular cod-end with 35 mm liner. For the biomass estimation the data on catch rate from 145 daytime tows were used, taking account the significant difference between the catch rates in the daytime and at night.

The biomass estimate at that time of the year and the corresponding 95 percent confidence interval were calculated following Mackett, 1973:

$$B = N \cdot \bar{X}$$

$$\bar{X} = \frac{\Sigma(N_h \cdot \bar{X}_h)}{N}$$

$$S_{\bar{X}} = \sqrt{\frac{1}{N^2}\,\Sigma\, N_h\,(N_h - n_h)\cdot\frac{s_h^2}{n_h}}$$

95 percent confidence interval = $N\,(\bar{X} \pm t_{0.05} \cdot S_{\bar{X}})$

B = standing stock size
$\bar{X}$ = estimated population mean (mean catch per haul)
$\bar{X}_h$ = sample mean within stratum h (mean catch per haul within stratum h)
$S_{\bar{X}}$ = standard error of $\bar{X}$
S_h^2 = sample variance within stratum h (variance of catch per haul within stratum h)
N = population size (value obtained by dividing the whole area by the mean area swept per haul)
N_h = population size within stratum h (value obtained by dividing the area of stratum h by the mean area swept per haul)
n_h = number of samples within stratum h (number of hauls in stratum h)
$t_{0.05}$ = student's t value in the degree of freedom (total number of samples - number of strata)

The area swept per haul was calculated from the distance towed, and the width between both net wings was as follows:

mean area/haul = 0.033 n mi²
standard deviation = ± 0.00343 n mi²
range = 0.022 - 0.044 n mi²

The net coefficient was arbitrarily assumed to be 1.0, i.e., assuming that almost all squid near the bottom of the area of sea floor swept were taken by the trawl (with 35 mm liner inside the codend).

The results obtained are shown in Table 9. The standing stock size was estimated to be around 30 600 t with a 95 percent confidence interval of ± 7 100 t. The corresponding standing stock size in number was estimated from the size compositions of the catch at

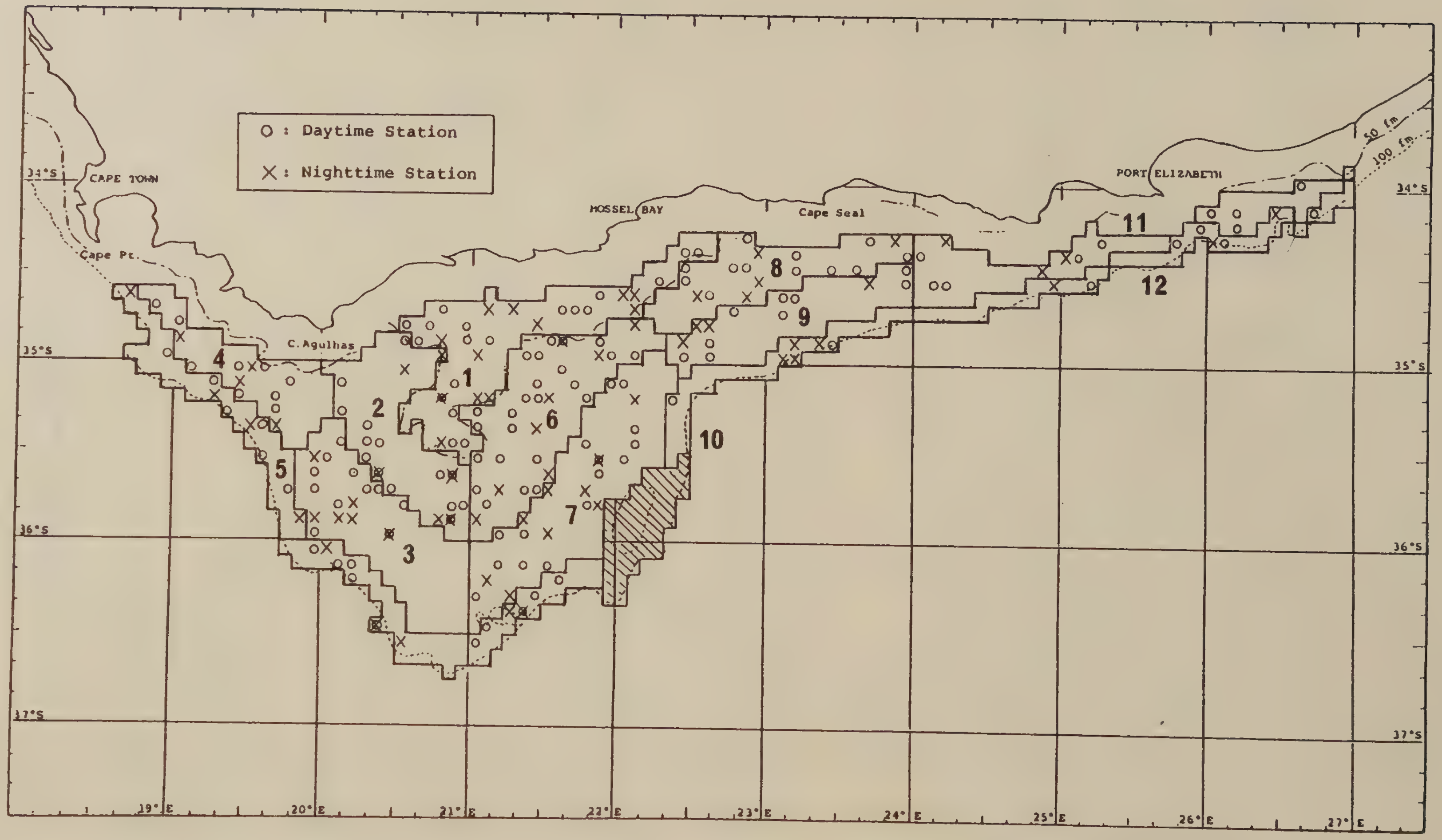

O : Daytime Station
X : Nighttime Station
CAPE TOWN
Cape Pt.
C.Agulhas
MOSSEL BAY
Cape Seal
PORT ELIZABETH
50 fm
100 fm
34°S
35°S
36°S
37°S
19°E
20°E
21°E
22°E
23°E
24°E
25°E
26°E
27°E
1
2
3
4
5
6
7
8
9
10
11
12

Figure 4 Location of stations trawled during the Japan/South Africa joint trawling survey in November/December 1980. The shaded area was eliminated from the survey because it was deeper than 100 fathoms. Numerals in the figure denote stratum numbers

Table 9

Biomass and stock size in number of long-finned squid, *Loligo reynaudi*, on the Agulhas Bank estimated by the areal expansion method

Stratum	Area (naut. mile[b])	Ave. CPUE (kg/haul)	Biomass (in tons)	Stock size in number (10^4)			
				Small[a]	Medium[a]	Large[a]	Total
1	2 216	38	2 307	6 921	1 700	997	9 618
2	1 691	62	3 155	83	861	2 223	3 168
3	1 881	109	6 174	14	1 074	4 110	5 199
4	1 207	69	2 521	3	567	1 676	2 246
5	1 625	116	5 701	-	187	2 974	3 161
6	2 225	18	1 431	284	802	426	1 512
7	2 414	21	1 500	12	99	867	978
8	1 422	31	1 374	660	543	767	1 971
9	1 356	37	1 523	1 096	962	937	2 995
10	1 116	37	1 245	-	2	622	625
11	1 549	56	2 625	223	200	1 840	2 263
12	949	35	1 005	93	129	792	1 013
Total	19 651	49	30 561	9 390	7 126	18 232	34 749
Confidential intervals[b]			± 7 091	± 8 438	± 2 137	± 4 823	±10 251

[a] Size categories of squid in mantle length

Small ; under 8 cm, Medium ; 8 - 13 cm, Large ; over 13 cm

[b] The 95 % confidential intervals

each trawl station and the mean weight of squid for each size class at 1 cm intervals. The resultant stock size in number by size categories in each stratum shown in Table 9 suggests that the small-to-medium sized and large sized squid were mainly distributed in waters shallower than 50 fathoms, and at depths between 50 and 100 fathoms, respectively, and the stock density in weight on the western half of the Agulhas Bank (strata 2, 3, 4 and 5) was considerably higher than that on the eastern half (strata 6, 7, 8, 9 and 10).

In the light of the common feature of general distribution of loliginid squid in the world, this squid is considered to be a coastal species originating from the spawning grounds in the coastal waters. It is also assumed that the main habitat of this species is confined to the waters on the continental shelf and upper slope; the young and small squid progressively extending their habitat to offshore waters on the Agulhas Bank as they grow larger. Most surviving adult squid return to the coastal waters for spawning before dying.

The foregoing three size categories of small, medium and large (Table 9) correspond to three different length groups observed in the measured size compositions of the catch at each trawl station, which would suggest the existence of three different seasonal broods of squid at least among the catch, but the proportional stock size in number of 'small' (27 percent) and 'medium' (21 percent) to the total estimate were fairly low comparing to that of 'large' squid (52 percent). This abnormally low proportion of small-to-medium squid in the standing stock size by number in the survey area might suggest their possible existence in large quantities in coastal waters, including the South African territorial waters, excluded from this survey.

If this assumption is correct, a notable underestimation of the biomass must have been made due to incomplete coverage of the species habitat. In relation to this underestimation introduced, two more problems could be pointed out. The first is that the actual measurement of the percentage of squid actually taken from those on or near the bottom in the area swept by the trawl gear, is virtually impossible. The second problem is that squid are distributed not only at the bottom but also in mid-water, and the proportion of squid in mid-water is unknown.

In the survey, the vulnerability with regard to the bottom trawl was assumed to be 1.0 for convenience, and only the catch and CPUE data on the squid existing from the bottom to the net height of approximately 5-8 m were used for the biomass calculation, regardless of those squid that must also be distributed in the upper layers of the ocean in the survey area. Therefore, the standing stock size must have been considerably underestimated.

Sissenwine and Tibbetts (1977) estimated that 0.40 was the optimum value (E_{MSY}) for the rate of exploitation of *Loligo* squid in the NAFO area, on the basis of the stock-recruitment relationship; $R = P/[1 + a(P - 1)]$ (Beverton and Holt, 1957); using an arbitrary choice of $A = 0.8$ (indicating a moderate degree of relationship between spawners and progeny), and this value has been used to date for the determination of the annual catch limit (TAC) for chokker squid also. Therefore, assuming that the E_{MSY} value of 0.40 is applicable to chokker squid, a potential yield of this species could be roughly estimated by multiplying the possible biomass by 0.40.

The period from mid-November towards the beginning of December 1980, when the biomass survey was carried out, corresponded to the beginning of the main fishing season for this squid. Therefore, taking account of the rapid growth in weight of this species, as well as the foregoing causes of underestimation in the survey, the resultant biomass of 30 600 ± 7 100 t at the time of the year of the survey was probably very conservative.

However, given that no better estimate was available, the conservative biomass estimate is equivalent to a potential yield of 12 200 ± 2 800 t, which is rather higher than the annual catch limit (about 7 000 t) for 1981 established by South Africa.

2.3 Stock Assessment of the Arrow Squid, *Nototodarus sloani*, in New Zealand Waters

The arrow squid, *Nototodarus sloani*, is widely distributed within most parts of the 200-mi Exclusive Economic Zone of New Zealand (Figure 5), and is believed to be composed of several local stocks. The number and extent of these hypothetical local stocks is not established yet, and so far their migrations are not well understood. Each of the possible local stocks seem to make an independent seasonal migration with repeated intermingling and separation from one another, and occasionally big concentrations are formed down to about 300 m in depth, near the bottom, or in the middle to upper layers of the sea. Furthermore, arrow squid are believed to be the most abundant and predominant species of all squid in New Zealand waters and almost all squid taken by trawlers and jigging vessels seem to be of this species.

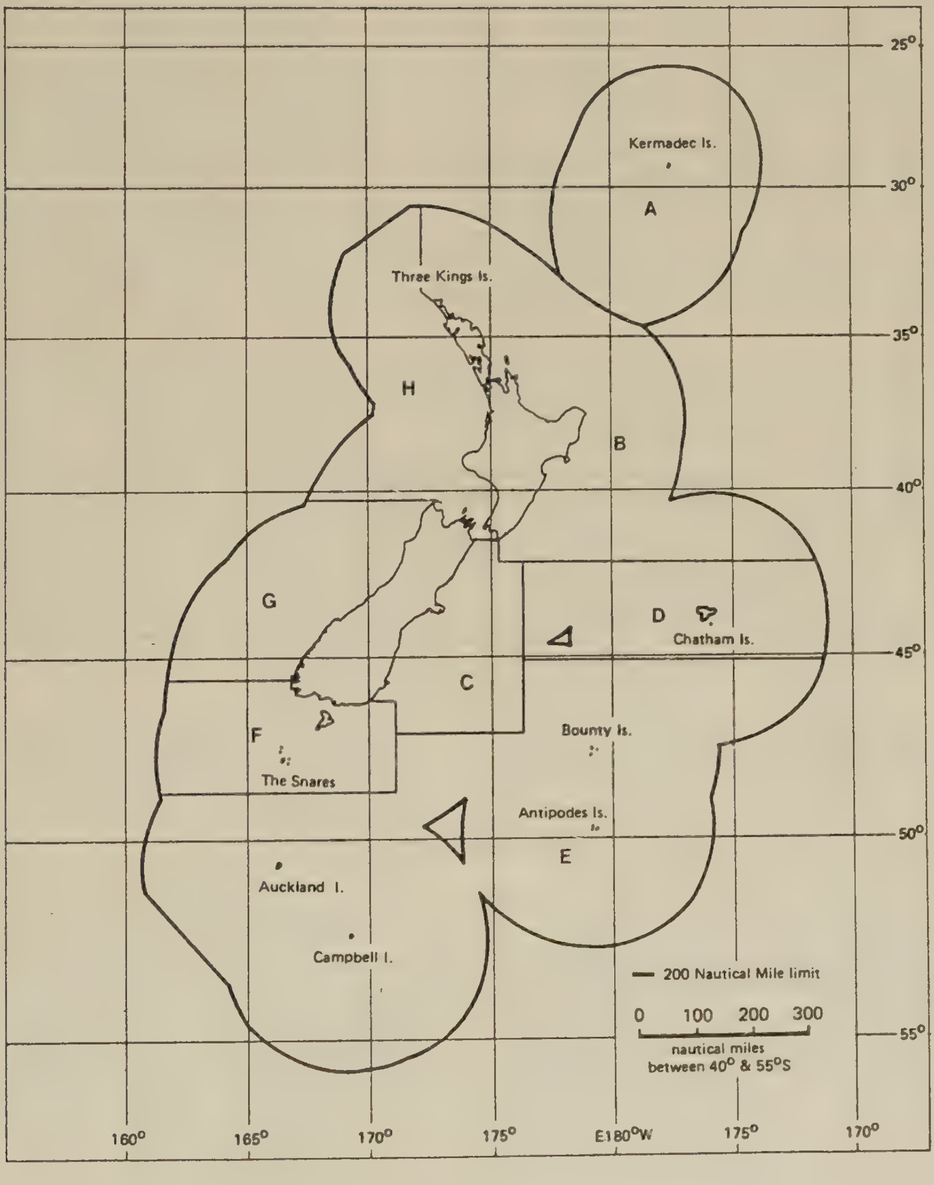

25°
Kermadec Is.
30°
A
Three Kings Is.
35°
H
B
40°
G
D
Chatham Is.
45°
C
F
The Snares
Bounty Is.
Antipodes Is.
50°
E
Auckland I.
Campbell I.
200 Nautical Mile limit
0 100 200 300
nautical miles
between 40° & 55°S
55°
160°
165°
170°
175°
E180°W
175°
170°

Figure 5 Chart showing New Zealand's 200-mi Exclusive Economic Zone and locality of Areas A-H

Annual catches (total and by countries) of arrow squid in New Zealand waters for 1970-80 are shown in Table 10. Japanese squid-jigging vessels exploited firstly some promising fishing grounds off the west coast of New Zealand, extending from the southwest coast of North Island to the northwest coast of South Island, and off the east coast of South Island (Areas G, H and Area C, respectively, in Figure 5), and embarked on a full-scale operation in 1973. Later on Japanese trawlers began taking this squid as one of the target species on the traditional fishing ground off the east coast of South Island. Subsequently, New Zealand, the USSR, and the D.P.R. of Korea began squid fisheries in 1977, though no clear information on their fishing grounds is available.

The annual total catch has substantially increased since 1973, and reached a peak of around 76 000 t in 1977 due to an increase in Japanese catch and a massive catch by the USSR, but showed a noticeable decrease thereafter mainly due to the maximum limit of squid catches by foreign trawlers established by New Zealand. No detailed information on squid fisheries by other countries being available, only the catch and effort data on the Japanese trawl and squid-jigging fisheries are shown in Tables 10 and 11, respectively.

The catch and CPUE by recent Japanese trawl fishery in each area showed a considerable year-to-year fluctuation (Table 11) and these fluctuations seem to have been caused by annual changes in recruitment of squid to the exploited stocks in each area, exclusive of Areas C and E. The sharp decreases in catch and CPUE in Area C after 1978 were caused by the closure of the main fishing grounds for squid to the Japanese trawl fishery enforced by New Zealand, and consequently the catch and CPUE in Area E increased sharply from 1979 onward through the exploitation of new fishing grounds on the offshore plateaux. However, no particular increasing or decreasing tendency is recognizable in the annual changes in CPUE for the overall area (Table 11).

Table 11 shows that the maximum catch of 41 000 t was attained in the 1977/78 fishing season by the Japanese squid-jigging fishery with the highest CPUE (catch per vessel day) of 3.83 t for the overall area of operation. The corresponding values of CPUE and the proportional catch and effort in each area are also shown in Figure 6, which indicates that the majority of annual catches by Japanese jigging vessels was taken in Areas C, G and H every year except for the 1979/80 fishing season. In the 1979/80 fishing season fishing conditions on most of the traditional fishing grounds were unusually bad, and thus many Japanese jigging vessels operated in Area F where many big concentrations of squid occurred in mid-water over the continental shelf south of Stewart Island. Consequently, about 52 percent of the annual catch by jigging vessels was taken in Area F in 1979/80, with the highest CPUE of 4.0 t/vessel-day, although no good concentrations of squid were observed there during the next season (Figure 6).

Although fluctuations in CPUE were observed in all areas operated, no particular trend was recognizable in the annual changes in CPUE for the overall area and the same was as for the trawl fishery (Tables 11 and 12), and this lack of a general trend in CPUE might suggest a sustainable level of fishing of squid stocks as a whole in recent years, in spite of probable fluctuations in recruitment to each area.

Relative to stock assessment of this species, only one preliminary study using an analytical model has been reported (Kawakami, 1976). According to Kawakami, the stock size at the beginning of the 1972/73 fishing season (about 90 days from January to March 1973), within the main fishing ground surrounded by a 41°S latitudinal line, a 170°E longitudinal line, and a 12-mi line off the northwest coast of South Island, was around 36 million by number. This estimate was obtained from the corresponding catch of 6.5 million squid by 44 Japanese squid-jigging vessels operated within the area by applying the exploitation rate of 0.18 estimated from the analytical model. However, the author pointed out that this figure might be quite conservative.

The exploitation rate for the period was calculated from the corresponding values of natural mortality (M = 0.40) and fishing mortality (F = 0.24). Both of these figures for mortalities were arbitrarily partitioned using the value for total mortality (Z = 0.64) estimated from the mean of the fraction surviving for every 10-day interval. Each of the fraction surviving was obtained by taking the ratio of stock indices for successive two 10-day intervals: the stock index for each interval being calculated by adding all catch rates by number on a 1°-square block basis. This method is evidently applicable only in

Table 10

Annual catches (total and by countries) of arrow squid, *Nototodarus sloani*, in the New Zealand waters (t)

Country	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980
Japan[a/]	353	46	728	19 121	21 583	20 846	25 521	47 143	35 554	25 385	50 001
New Zealand[b/]	100	200	300	700	509	302	371	888	1 950	7 697	+
USSR[b/]	-	-	-	-	-	-	-	26 837	3 112	14 708	+
Korea[b/]	-	-	-	-	-	-	-	1 473	2 756	1 111	+
Total	453	246	1 028	19 821	22 092	21 148	25 892	76 341	43 372	48 901	+

+ ; No statistics available

a/ Combined catch by both of the trawl and squid-jigging fisheries based on Japanese catch statistics

b/ Data from Yearbook of fisheries statistics, FAO (Vol.36-48)

Table 11

Catch (t) and CPUE[a/] (t/h fished) of arrow squid, *Nototodarus sloani*,
by Japanese trawlers[b/] in each fishing area

Area	1975		1976		1977		1978		1979		1980	
	Catch	CPUE	Catch	CPUE	Catch	CPUE	Catch	CPUE	Catch	CPUE	Catch	CPUE
B	1	-	-	-	-	-	-	-	-	-	-	-
C	3 061	1.00	2 178	1.52	19 761	1.54	304	0.30*	2 432	0.31	71	0.17
D	1	-	2	-	1 038	1.33	1 068	0.17	252	0.10	349	0.08
E	129	0.24*	837	0.86	38	0.80*	62	-	2 415	1.67	22 652	1.63
F	175	0.49	1 056	0.75	181	0.28	179	0.05*	294	0.15	915	0.35
G	45	-	26	0.00	251	0.13	63	0.50	44	0.16*	9	-
H	56	-	159	-	513	0.12	1 116	0.52	227	0.04*	124	0.26*
Total	3 469	0.98	4 256	1.26	21 781	1.52	2 792	0.47	5 675	0.51	24 120	1.53

a/ CPUE by large-sized trawlers (over 2 000 GRT) engaged in the squid directed fishery

b/ Including some trawlers operating under the Japan/New Zealand joint venture

* CPUE by medium-sized trawlers (1 001-2 000 GRT) substituted for that by large-sized ones

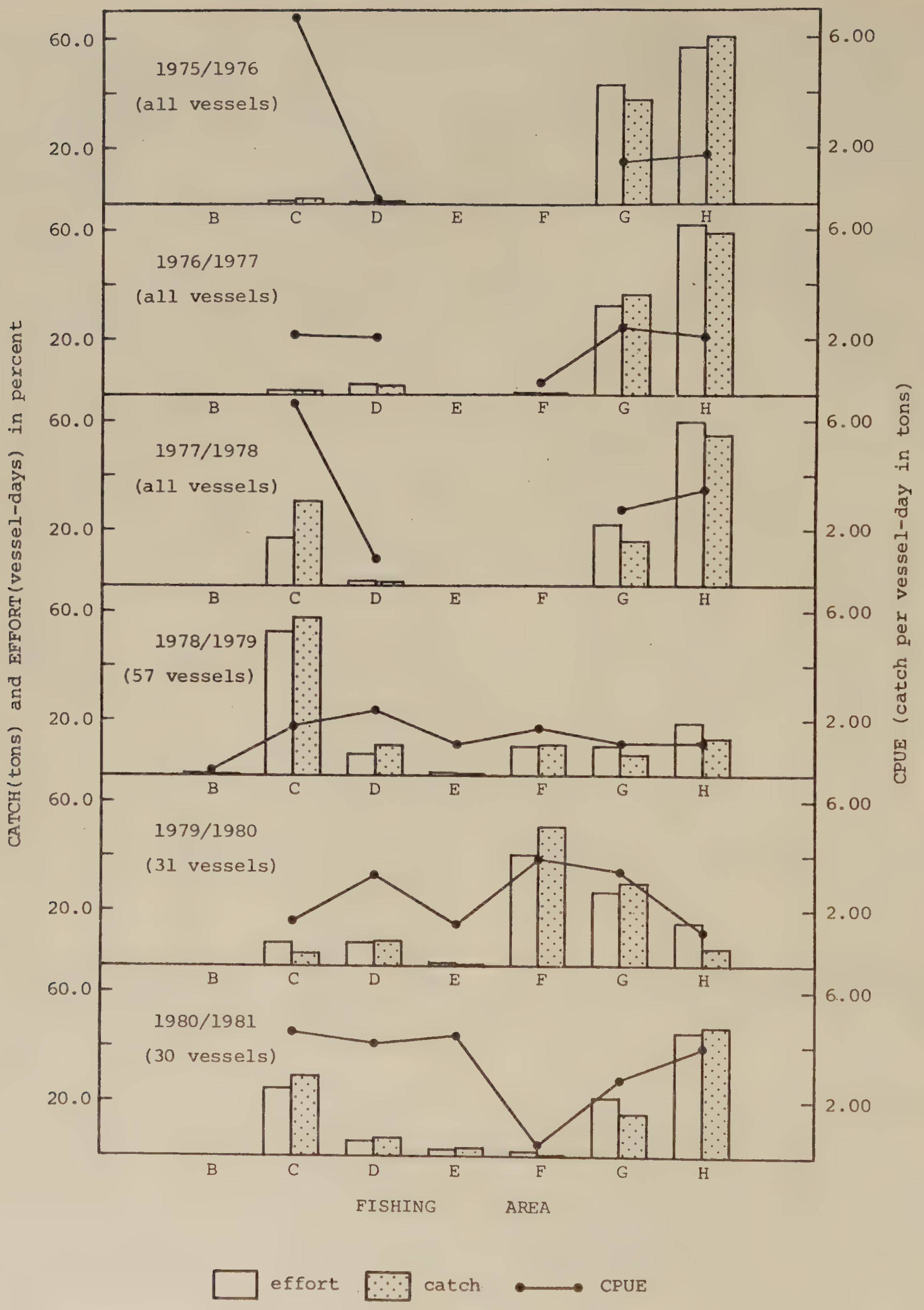


Figure 6 Annual changes in squid catch (t), effort (vessel-days) and CPUE (catch per vessel-day) by Japanese squid-jigging fishery, 1975/76-1980/81

Table 12

Catch and effort data on arrow squid, *Nototodarus sloani*, taken by Japanese squid-jigging fishery in New Zealand waters for the fishing years 1973/74-1980/81

Fishing year	1973/1974	1974/1975	1975/1976	1976/1977	1977/1978	1978/1979	1979/1980	1980/1981
Period of fishing	Nov.,1973 -May, '74	Nov.,1974 -Apr.,'75	Nov.,1975 -Apr.,'76	Dec.,1976 -May, '77	Dec.,1977 -Mar.,'78	Dec.,1978 -May, '79	Dec.,1979 -May, '80	Dec.,1980 -Apr.,'81
Number of vessels operated	156	151	128	126	127	113	98	71
Total vessel-days fished	9,536	11,698	11,988	11,473	10,676	11,561	8,748	5,927
Total catch in tons	14,761	18,947	19,598	25,571	40,924	18,220	25,150	22,462
Catch per vessel in tons	94.6	125.5	153.1	194.4	303.3	161.2	256.6	316.4
Catch per vessel -day in tons	1.55	1.62	1.63 W : 1.63 E : 0.50	2.23 W : 2.14 E : 1.97	3.83 W : 3.17 E : 5.98	1.58 W : 1.15 E : 1.83	2.87 W : 2.57 E : 3.40	3.75 W : 3.56 E : 4.27

W ; West coast including Areas G and H,
E ; East coast including Areas C,D,E and F.

the case that the squid schools in a particular area are composed of a single stock and the stock size in number shows a gradual decrease with time. In most of the wide-ranging fishing grounds for recent squid fisheries however, the size compositions of squid taken and hence the catch in number usually show geographical, seasonal, monthly and/or weekly fluctuations with, or sometimes independent of, changes in catch by weight. Accordingly, the foregoing analytical model is very difficult to apply and such a complexity of fluctuations in recruitment and intermingling of possible different populations combined with a very short life span for this squid, in addition to our poor knowledge of local stocks and their migrations, have prevented the progress of stock studies by analytical methods.

In such a situation, the areal expansion method, a technique for quick assessment by the use of CPUE data based on the stratified random sampling, seems to be the best way available for estimation of the standing stock size of this species. In this context, this method was adopted in the Japan/New Zealand joint squid survey carried out from January to March, mainly in February 1981, using a Japanese exploratory research vessel (Kawahara and Tokusa, 1981). The main objective of the survey was to estimate the biomass of arrow squid at the beginning of the fishing season in Areas E and F where Japanese trawlers are permitted to catch the squid in a directed fishery under a specific catch quota allocated by New Zealand.

The biomass survey was performed on the continental shelf and upper slope down to a depth of 600 m outside of the 12-m territorial waters, lying between 46°00'S and about 51°15'S, and covering 15 900 n mi². The trawl stations were selected by the stratified random sampling method; the survey area was divided into 2'-square blocks and these were stratified into 10 strata by three latitudinal lines (46°00'S, 48°30'S and 50°00'S) and three depth contours of 200, 400 and 600 m (Figure 8, right).

A total of 100 daytime stations were allocated among all strata in proportion to the size of each stratum. The area of the strata within the depth of 400-600 m was multiplied by a weighting factor of 0.5 and at least four stations were apportioned to each stratum. The positions of trawl stations were settled at random within each stratum on a 2'-square block basis (Figure 8, left). A 30-min trawling was carried out at each station only in the daytime, taking account the significant difference between the catch rates of squid in the daytime and at night.

The biomass estimate in the survey area at the time of the year and the corresponding standard error were calculated by the following equations:

$$B = \Sigma B_i \qquad S_B = \Sigma S^2_{B_i}$$

$$B_i = \frac{A_i}{a} \cdot \bar{X}_i \qquad S_{B_i} = \frac{A_i}{a} \cdot \frac{S_i}{n_i}$$

where: B = standing stock size within the overall survey area

S_B = standard error of B

B_i = standing stock size within stratum i

S_{B_i} = standard error of B_i

A_i = area of stratum i

$\bar{X}_i$ = mean catch per tow in stratum i

S_i = standard deviation of $\bar{X}_i$

n_i = number of tow in stratum i

a = average area swept by a tow

The average area swept per 30-min tow was calculated from the mean values of distance between the trawl wings in operation (= 31 m), height of the net mouth (= 6.2 m) and towing speed (= 3.4 kn), to be approximately 2.8×10^{-2} n mi².

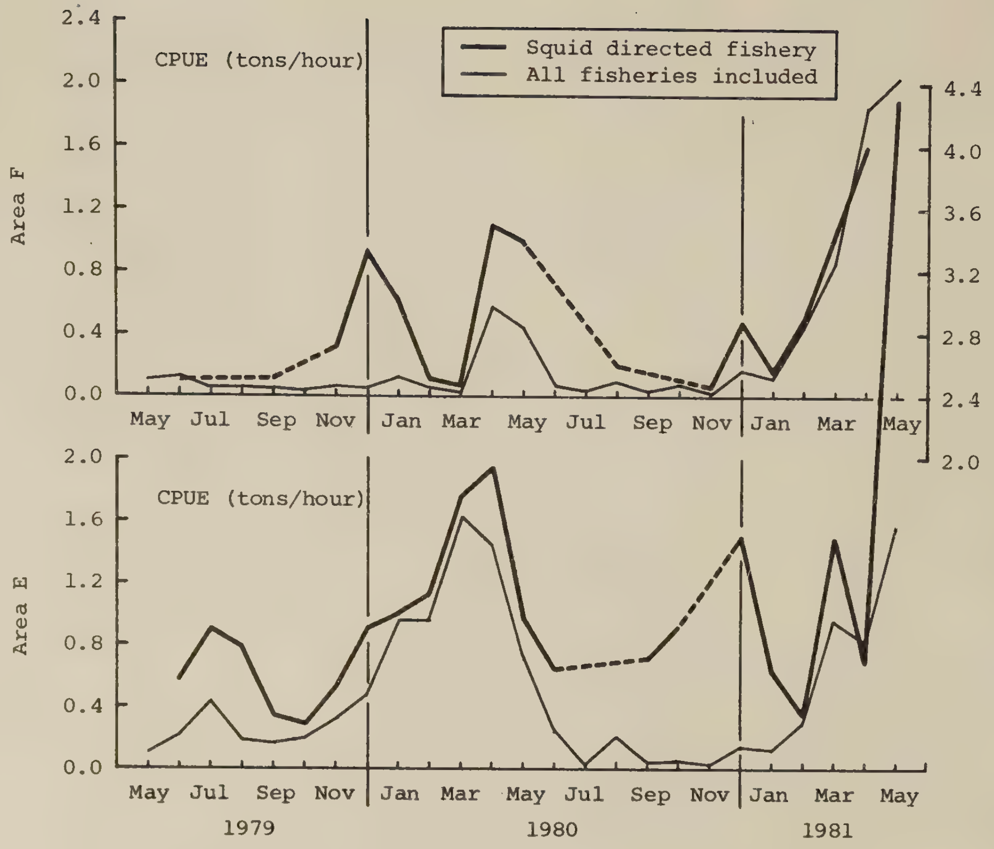


Figure 7 Monthly changes in squid CPUE by Japanese trawl fisheries in each of Area E and Area F for the period May 1979–May 1981

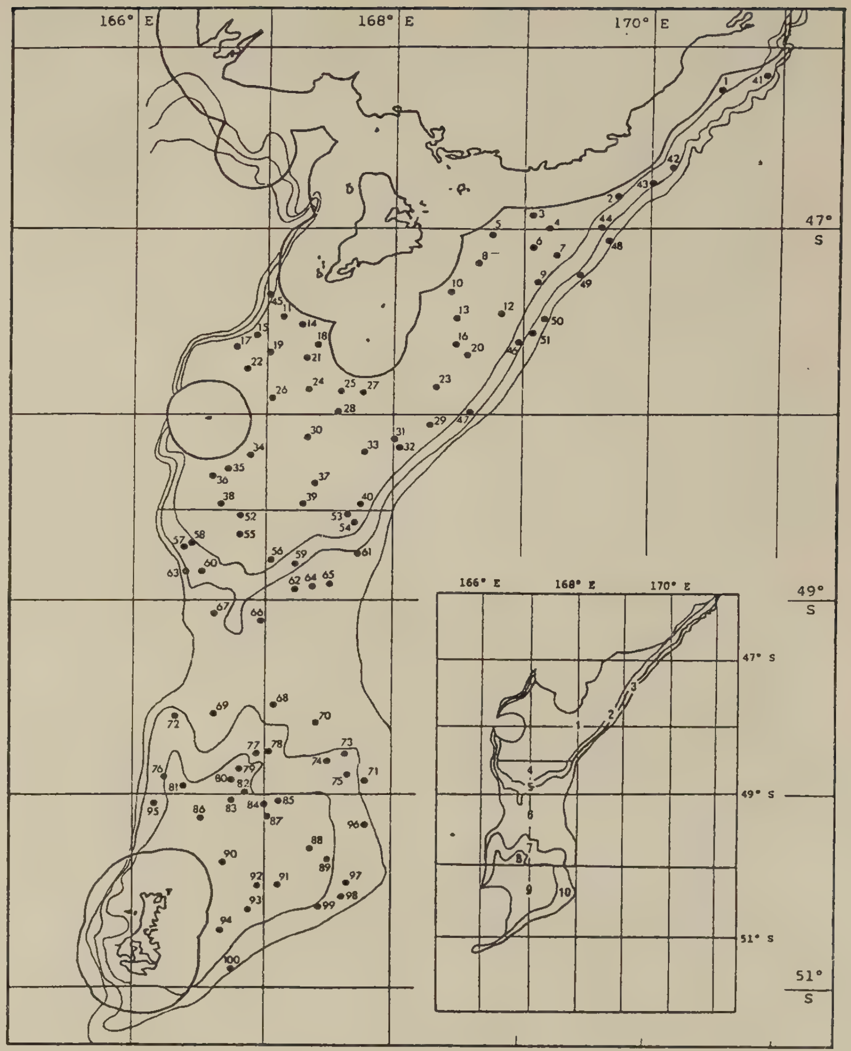

166° E
168° E
170° E
47° S
49° S
51° S
166° E
168° E
170° E
47° S
49° S
51° S

Figure 8 Localities of stations (left) and strata (right) for the squid trawling survey. Figures denote the station number (left) and the stratum number (right)

The mean mesh size of codends used varied from 62 to 81 cm. As it is considered that the selection factor (50 percent retention length/mesh size used) for this squid is about 2, more than half the number of squid taken smaller than about 14 cm in mantle length could escape through the codend. However, the catch in weight was probably minimally affected by the escapement even on the shelf in the northern part of the survey area where some small squid less than 14 cm were included among the catches. The net coefficient was thus regarded as 1.0 for convenience on the arbitrary assumption that almost all squid near the bottom in the area swept were caught by the trawl gear.

The resultant biomass estimates and corresponding standard errors are shown in Table 13. Biomass estimates in the daytime when squid were more vulnerable to the bottom trawl were 35 200 t in total; 9 500 t in Area F and 25 700 t in Area E.

However, this value of 35 200 t within the survey area in Areas E and F seems to be far lower than that expected from recent squid catches. This was attributed to the generally low value of CPUEs at most of the trawl stations except a few made in the present main fishing grounds around Auckland Island in Area E. Furthermore, the applications of a net coefficient of 1.0 and the restriction of the zone of capture to squid occurring from bottom to a net height of about 6.2 m, regardless of those in the upper layers of the survey area, must also have led to considerably underestimated values.

The period of the squid survey in 1981 was decided in the light of fishing conditions for the directed fishery during the corresponding period in 1980, when the squid catch by Japanese trawlers began increasing sharply with a moderately high value of CPUE, especially in Area E. However, contrary to expectation, the seasonal CPUEs of squid, as well as the catches by Japanese trawlers, were very low in 1981 throughout the period of the trawling survey, from late in January to early in February in Area F and from mid-February to early in March in Area E, compared to the corresponding values in the previous year (Figure 7). These facts might suggest that the catchable stocks of squid were unusually poor, as a whole, in Areas E and F at the time of the year when the biomass survey was carried out.

The Japanese squid fishery, late in 1981, was characterized by substantial increases in CPUE from March in Area E and from February in Area F, up to May (Figure 7). Such a simultaneous recovery of fishing conditions in both Areas E and F from March onwards, might indicate a general increase in catchable stocks for the two adjacent areas during the period, although the timing does not necessarily suggest a close relationship between the squid populations involved.

Accordingly, it could be concluded that the abnormally low abundance of squid in the established fishing grounds extending over Areas E and F up to February 1981 was mainly due to the delay in the massive recruitment of squid into the catchable stocks and that the subsequent recoveries in the catch and catch rates to the directed fishery in each area might suggest a rather healthy state of squid stocks concerned in spite of the unexpectedly low biomass estimate resulted from the 1981 squid survey.

2.4 Stock Assessment of Short-Finned Squid, *Illex argentinus*, off the Coast of Argentina

The Argentine species of *Illex*, *Illex argentinus*, is believed to be the most abundant and predominant species of all the squid in the southwest Atlantic, but the scope of geographical distribution within the area is not well understood. Nevertheless, it seems that the majority of them inhabit the continental shelf and upper slope between 80 m and 800 m depth, and between 35°S and 54°S (Castellanos and Menni, 1969), off Argentina where almost all of the annual catches have been taken by trawlers from several countries.

Annual catches (total and by countries) of this species for the years 1967-80 are shown in Table 14. Until 1977 this squid was taken by both Argentina and Uruguay as a hake fishery by-catch, and total annual catches remained at no more than 8 300 t. The total squid catch showed a major increase thereafter, and reached about 69 000 t and 107 000 t in 1978 and 1979, respectively. This sharp increase in total catch from 1978 onwards was mainly due to the start of a full-scale squid fishery by Argentine trawlers transferred from the traditional hake fishery, and the participation of Japanese trawlers in the fishery.

Table 13

The results of a biomass survey on the arrow squid, *Nototodarus sloani*, in the current main fishing grounds for Japanese trawl fishery using the areal expansion method

Fishing Area	Stratum	Depth range (m)	Area (sq. n. miles)	Number[a] of tows	Mean of CPUE's (kg/half hour)	Biomass estimates in tons	
						Biomass	Standard Error
F	1	-200	5 799	40	43	8 800	2 100
	2	200-400	974	7	17	600	200
	3	400-600	710	4	4	100	50
E	4	-200	716	5	180	4 600	2 700
	5	200-400	577	4	280	5 800	1 600
	6	400-600	3 199	11	12	1 400	500
	7	200-400	975	7	63	2 200	1 300
	8	-200	243	4	355	3 100	1 300
	9	-200	1 797	12	94	6 000	4 100
	10	200-400	891	6	82	2 600	2 000
Total			15 881	100	62.1[b]	35 200	6 200

a/ Daytime operations
b/ Stratified mean

Table 14

Catches (total and by countries) of short-finned squid, *Illex argentinus*, in the southwest Atlantic (in t)

Country	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980
Argentina[a]	2 262	2 874	882	1 345	1 701	1 573	3 933	4 916	4 132	7 493	2 168	59 001	86 869	+
Uruguay[b]	-	-	-	100	100	200	200	100	520	773	362	2 182	4 668	+
Japan[c]	-	-	-	-	-	-	-	-	-	-	1	6 908	14 903	6 140
Poland[b]	-	-	-	-	-	-	-	-	-	-	3	4 366	15 048	+
Germany, F.R. of[b]	-	-	-	-	-	-	-	-	-	-	-	664	559	+
German D.R.[b]	-	-	-	-	-	-	-	-	-	-	-	-	156	+
Total	2 262	2 874	882	1 445	1 801	1 773	4 133	5 016	4 652	8 266	2 534	73 121	122 203	6 140

+ No statistics on the squid catch is available
a/ Statistics by Argentine Government
b/ Yearbook of Fishery Statistics, FAO (Vol.36-48)
c/ Data from the Far Seas Fisheries Research Laboratory, Japan Fishery Agency

Japanese trawlers operated in Argentine waters on an experimental basis in 1978 under the Japan/Argentina fishery agreement, but thereafter they shifted to waters outside the 200-mi limit, and have since been operating a directed squid fishery in the open sea. The Japanese figures for CPUE of this squid by large-sized trawlers (3 500-4 000 GRT) in each of the 1978 and 1979 fishing seasons (April-July) were 2.3 and 3.8 t/h, respectively, but decreased sharply to 0.5 t/h in 1980. However, fishing conditions showed a favourable turn in the 1981 fishing season and yields increased greatly; it is estimated that they will exceed 20 000 t and the corresponding mean CPUE will also be considerably high. Such a change in catch rate would suggest a wide-ranging year-to-year fluctuation in the recruitment of squid populations, independent of the fishery.

No stock study on this species was reported before 1971 except one, by Hempel (1970), in which a catchable stock size of several hundreds of thousands of tons in the southwest Atlantic was suggested. In these circumstances, Japan carried out a scientific fishery resources survey jointly with Argentina in the Argentine waters for one full year from April 1978, using R/V SHINKAI-MARU (Japan Marine Fishery Resource Research Center, 1979).

One of the main objectives of the joint survey was the estimation of the standing stock size of commercially important bottom species including this squid. The survey was composed of 12 successive cruises and the biomass estimation of the squid was performed for each pair of the first/second, fourth/fifth and tenth/eleventh cruises, which corresponded to each season of autumn (April-June), winter (July-September) and summer (January-March), respectively.

Each of three pairs of cruises covered almost the entire Argentine waters for the grid survey by bottom trawls (Figure 9). The trawl stations were set in a grid of each degree of longitude and latitude, but some additional stations were operated on the continental slope where the distribution and abundance of squid are apt to change sharply. The number of trawl stations covered by the grid surveys in autumn, winter and summer were 155, 144 and 154, respectively. As an example, the location of trawl stations for the first and second surveys in autumn is shown in Figure 8. Throughout the survey cruises a 30-min trawling was carried out at each station for the biomass survey using a codend with 100 mm mesh (doubled).

The main reason why a grid survey was employed for the biomass estimation was that the available information on oceanographic conditions, topographies, the distributions and ecological characteristics of Argentine *Illex* and other important demersal fishes was still insufficient for the application of a stratified random sampling method.

On the basis of the squid catch and effort data by such a trawling at each station, the standing stock size was estimated using the following equation:

$$B = \Sigma (A_i \cdot X_i / l_i \cdot w_i) / 1\,000$$

where: B = standing stock size (t)

A_i = area of the block represented by i-th station (n mi²)

X_i = catch per haul at i-th station (kg)

l_i = distance hauled at i-th station (n mi)

w_i = width between wings of trawlnet in operation at i-th station (n mi)

The area of each block on the continental slope was prearranged in an irregular fashion by calculating the area enclosed by lines drawn between stations and a given depth contour. The width between wings of the trawlnet was estimated at every operation from the developing angle of warp and the net coefficient was arbitrarily considered to be 1.0.

The resultant estimates of standing stock size in three different seasons are shown in Table 15. Taking account of the differences in the observed species composition of bottom fishes among three latitudinal zones, both the total and regional biomass estimates in each season are presented in the Table. The total estimates changed greatly from

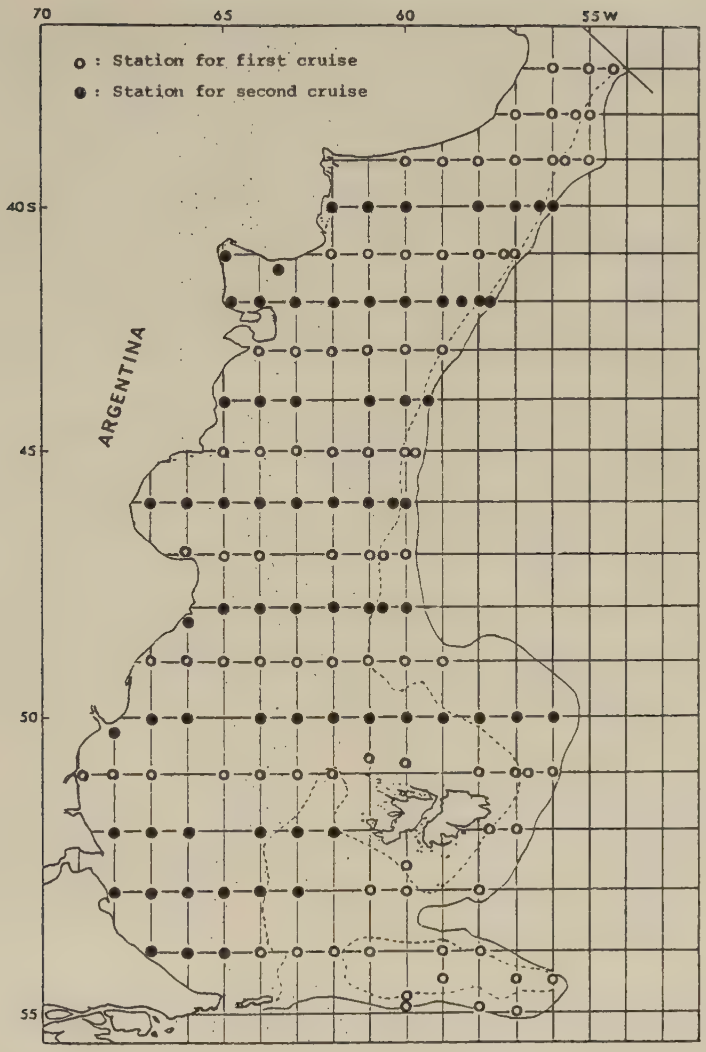

70
65
60
55W
40S
45
50
55
o : Station for first cruise
● : Station for second cruise
ARGENTINA

Figure 9 Locality of trawl stations for the first (10 April-9 May) and second (13 May-11 June) cruises by R/V SHINKAI MARU in 1978. Depth contours of 50 and 100 fathoms are represented by the broken and solid lines, respectively

Table 15

Biomass estimates of short-finned squid, *Illex argentinus*, in the Argentine waters by grid survey

('000 t)

Region	Area (n. mile^2)	Autumn Apr 11-Jun 7 1978	Winter Jul 16-Sep 14 1978	Summer Jan 13-Mar 12 1979
Northern area (37°S - 40°S)	45 000	271	98	32
Middle area (40°S - 47°S)	120 000	1 892	81	195
Southern area (47°S - 54°S)	182 000	442	2	713
Total	347 000	2 605	181	940

2 605 000 t in autumn to 181 000 t in winter, and again to 940 000 t in the summer of the next year, with the maximum regional values of 1 892 000 t from the middle region in autumn, 98 000 t from the northern region in winter and 713 000 t from the southern region in summer.

This wide-ranged fluctuation of estimates seems to be closely connected with the seasonal changes in migration and stock density of this species in the survey area. The spawning season was estimated to be in winter to early spring from the seasonal changes in gonad condition of the catches. Furthermore, the seasonal and geographical changes in catch, catch rate and size composition of this species suggested a life cycle where the young and small squid born in winter to early spring in oceanic waters migrate onto the continental shelf and upper slope, growing up quickly into the maximum stock size in weight in late autumn, before most of the adult squid make an offshore migration into oceanic waters toward mid-winter for spawning before dying.

This would therefore indicate that the sharp decrease in biomass estimate in winter was mainly due to the dispersion of squid schools from the survey area for spawning and that the main stock in the summer of 1979 belonged to a different year-class from those in the former seasons in 1978. On this assumption, the standing stock size of 2 605 000 t in autumn was regarded as the most appropriate estimate available.

Sissenwine and Tibbetts (1977) estimated the optimum rate of exploitation (E_{MSY}) of *Illex* squid in the NAFO area to be 0.37 on the basis of the stock-recruitment relationship; $R = P/[1 + A(P - 1)]$ (Beverton and Holt, 1957) using an arbitrary choice of $A = 0.8$ for a moderate spawner-recruit dependence, and this value of E_{MSY} has been maintained to date to determine the annual catch limit (TAC). Assuming that the foregoing E_{MSY} value is applicable to this species also, a potential yield of this species could be roughly evaluated by multiplying the possible biomass by 0.37.

The standing stock size of 2 605 000 t might have been a considerable underestimate of the maximum biomass estimate for 1978 in the survey area, because the net coefficient was assumed to be 0.1 in the calculation of CPUE and only the catches of those squid occurring between bottom and about 7.5 m were used for the analysis regardless of those squid also found in the upper layers of the survey waters.

Nevertheless, taking into account the low reliability of estimated stock sizes by means of grid survey and a very high abundance of squid stock in 1978, a half of the estimated value (= 1 303 000 t) could be arbitrarily adopted as a possible virgin stock size for the calculation of potential yield. Accordingly, the conservative estimate of virgin stock size gave a potential yield of 482 000 t, which is considerably higher than the annual total catches of this species from both of the Argentine waters and the open sea in recent years.

2.5 Stock Assessment of Cuttlefish, *Sepia* spp., off the Coast of the PDRY

Four Sepiid cuttlefish are commonly found on the continental shelves in the Arabian Sea extending from Oman to Somalia. These are three species of *Sepia*, namely *Sepia pharaonis*, *S. savignyi* and *S. prashadi*, and one species of *Sepiella inermis*. Among them, *Sepia pharaonis* seems to be the most abundant and predominant in the catch of cuttlefish from the present fishing grounds. According to Aoyama and Nguyen (1979), among 1 798 specimens of cuttlefish obtained from Japanese commercial catches for biological studies, 1 715 individuals were identified as *Sepia pharaonis* (95 percent), four specimens were *S. savignyi* (0.2 percent), and only one specimen was *S. prashadi*.

A full-scale cuttlefish fishery in the Arabian Sea was started by Japanese trawlers in 1967. The Japanese cuttlefish fishery was carried out all over the coastal waters extending from Oman to Somalia in the early stage of exploitation up to 1973, and thereafter operations have concentrated off the coast of the PDRY where the most promising fishing grounds for *Sepia pharaonis* were exploited. On the other hand, the foreign trawlers fishing under the PDRY/USSR joint venture, from Yemen and from the USSR participated in the cuttlefish fishery off Yemen in 1971, 1972 and 1980, respectively.

Catch and effort data on the Japanese cuttlefish fishery are available since 1967, but recent catches by foreign fisheries are estimated from the information on foreign catches collected by those Japanese fishing companies concerned as the most realistic figures. The annual total catch of all countries increased from about 4 200 t in 1967 to 15 500 t in 1977, but sharply decreased thereafter to 9 500 t in 1980 due to a noticeable drop in CPUE.

Ikeda (1975) evaluated the maximum equilibrium yield of cuttlefish off Yemen by applying the Schaefer production model to the stock on the basis of Japanese CPUE and standardized fishing effort for the years 1967-74. Sato (1977) repeated the same estimation on the basis of the revised CPUE and effort data for the years 1967-76. The resultant estimates of MSY were about 5 800 t with an effort of 1 300 days and around 6 500 t with 1 100 days, respectively, and both of the authors considered that the states of stocks were rather healthy and the fisheries were operated at around the optimum levels.

Subsequently, Aoyama and Nguyen (1979) have reported more recent work, involving the determination of Japanese standardized CPUE (catch in t/day), where they calculated the standardized fishing effort (in days) deployed by each Japanese vessel on a yearly basis for 1967-78 with due regard to the differences in fishing efficiency between a traditional standard medium-sized trawler and others. The ratio of fishing efficiencies made it possible to express the Japanese fishing effort and hence the CPUE in standard terms. The average fishing efficiency of the Japanese cuttlefish fishery since 1974 was estimated to be 1.3 times that of the fishery in the earlier years. The total standardized effort was thus calculated annually by multiplying the ratio of the catch of all countries to Japanese catch by Japanese standardized effort. Accordingly, the standardized CPUE was calculated annually by dividing the catch of all countries by the corresponding total standardized effort.

To assess the state of the stock, the Schaefer production model was applied and the CPUE was related to the effort in the same year on the assumption that the stock density of spawners and that of their recruits (combined catch of 0 and 1 age cuttlefish) show no clear relationship (Figure 10).

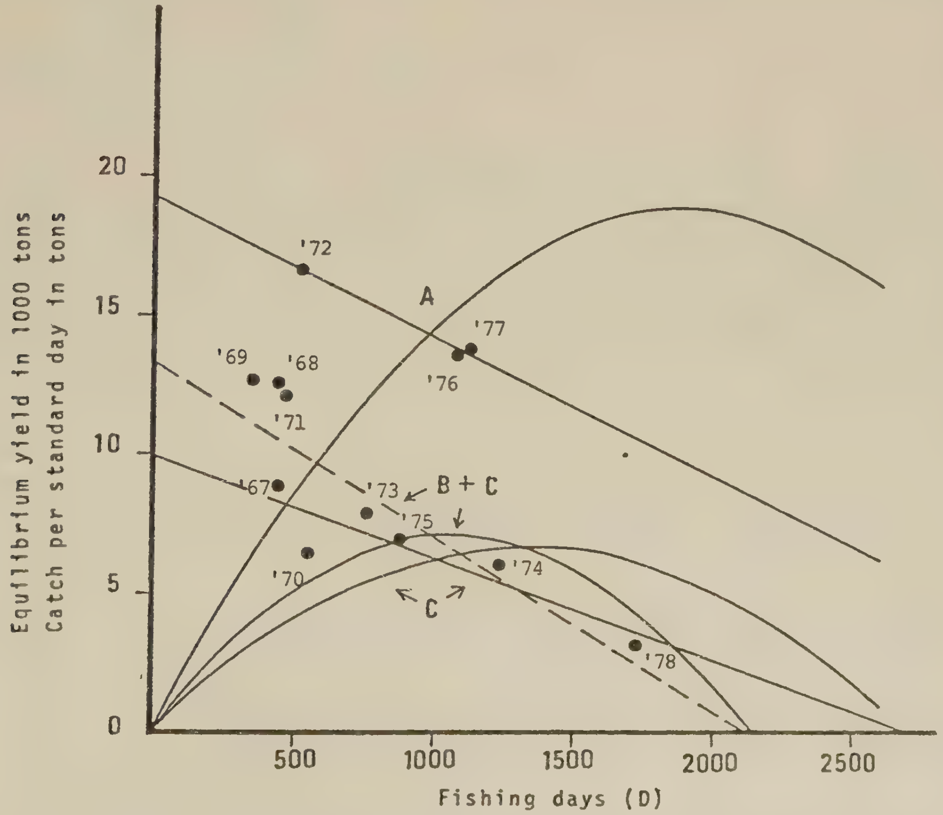


Figure 10 Relationship between CPUE (catch per standard day) and fishing effort (standardized days) and sustainable yield curves for cuttlefish off the PDRY

Table 16

Catch, catch per day and fishing effort for cuttlefish off the coast of the PDRY

Year	Catch in 1000 tons					Jpn.CPUE[c] in tons per day	Standard effort in days	2 yrs running effort ave.(days)
	Japan	PDRY[b]	J.V[a][b]	USSR[b]	Total[b]			
1967	3.8[b]	-	-	-	3.8	8.9	427	-
1968	5.6[b]	-	-	-	5.6	12.6	444	436
1969	4.53	-	-	-	4.5	12.7	354	399
1970	3.43	-	-	-	3.4	6.4	531	443
1971	5.33	-	0.5	-	5.8	12.1	479	505
1972	8.05	0.5	0.5	-	9.1	16.7	545	512
1973	5.01	0.5	0.5	-	6.0	7.9	759	652
1974	5.91	1.0	0.5	-	7.4	6.0	1233	996
1975	4.16	1.0	0.8	-	6.0	6.9	870	1052
1976	10.29	2.5	2.0	-	14.8	13.7	1080	975
1977	9.48	4.0	2.0	-	15.5	13.8	1123	1102
1978	2.33	1.0	1.0	-	5.3	3.1	1710	1417
1979	6.24	1.9	0.9	-	9.0	6.6	1364	1537
1980	3.90	2.2	2.2	1.2	9.5	6.2	1532	1448

[a] PDRY/USSR joint venture

[b] Estimated values cited from Aoyama and Nguyen (1979) and the data collected by the Nichiro Fish. Co., Ltd.

[c] Data from Aoyama and Nguyen (1979) and the Nichiro Fish. Co., Ltd.

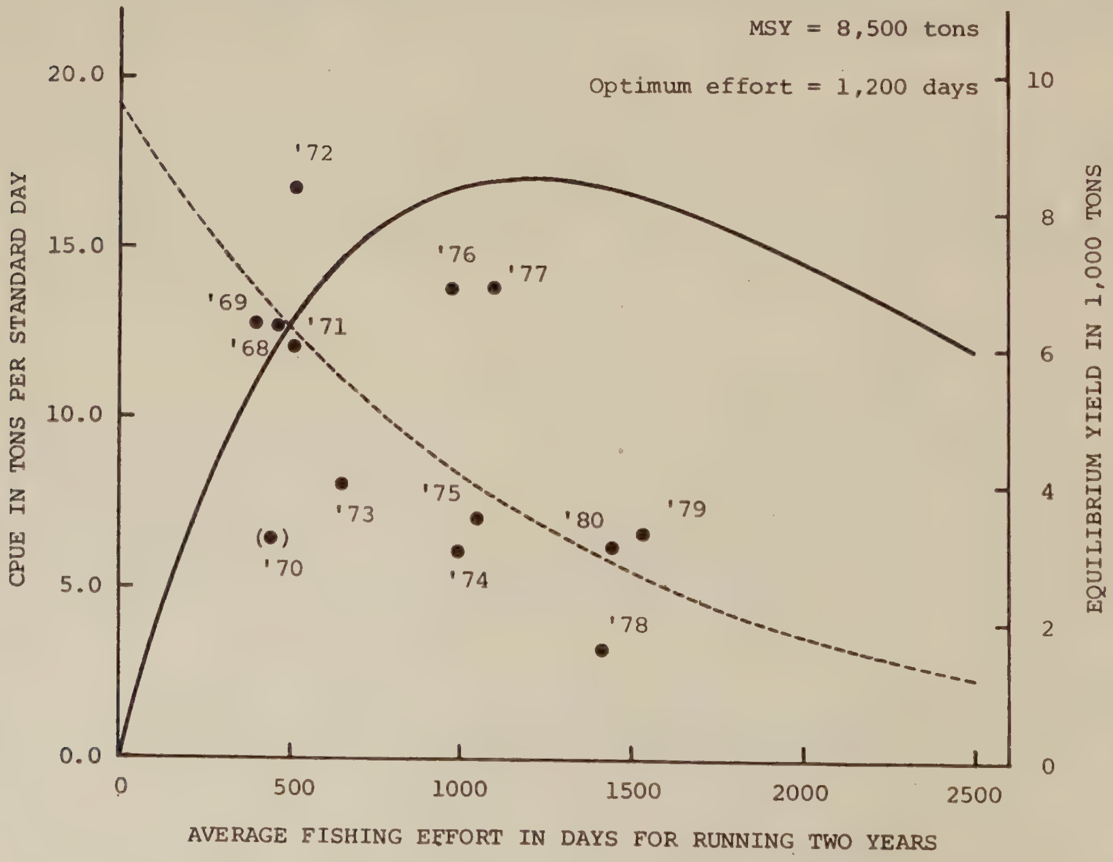


Figure 11 Relationship between CPUE and fishing effort (broken line) and sustainable yield curve (solid line) for cuttlefish off the PDRY (●); not included in the calculation

The resultant correlation coefficient was -0.60 with no clear relationship recognizable. A rough attempt was then made to classify the years on the basis of the quantity of resource available as follows:

A - extremely high resource years:	1972, 1976 and 1977
B+C - all years with resource levels below A:	1968, 1969 and 1971
C - low resource years:	1967, 1970, 1973, 1974, 1975 and 1978

and the relation between yearly fishing effort and yearly CPUE of each of the above A, B+C and C was examined separately by fitting a regression line to each.

The resultant parabolic equilibrium yield curves showed that the MSYs are about 19 000 t with an effort of 1 800-2 000 days, 6 200 t with 1 400 days, and 7 000 t with 1 100 days for A, B+C and C, respectively (Figure 10). From the above mentioned considerations, the authors concluded in the report that the maximum equilibrium yield is about 20 000 t with an effort of 1 500-2 000 days for extremely high resource years, and 7 000 t with an effort of 1 400 days for low resource years. It was also concluded that when the resource level lay between these two levels, the value for equilibrium yield also lay somewhere between curves A and C in Figure 10.

Another approach was made by Sato using the Gulland-Fox production model on the basis of the catch and CPUE data given in Aoyama and Nguyen (1979), and by a Japanese fishing company for the years 1967-80 (Table 16). The total standardized effort deployed was estimated by dividing the catch of all countries by the Japanese standardized CPUE. The CPUE was related to the mean effort for successive two years running, on the assumption that the fishing effort deployed in a given year affects the stock densities of both 0 and 1 age cuttlefish to some extent in the course of the assumed 2-year life span.

The regression line is shown in Figure 11 and is given by the equation:

$$\mathrm{CPUE} = e^{2.9528 - 0.00083f}$$

where: CPUE = catch in t/day
f = standardized effort in days

The correlation coefficient is -0.70. This is not statistically significant because the true relation between effort and CPUE is not well established: one reason being the considerable year-to-year fluctuations in recruitment independent of fishing.

The resultant equilibrium yield curve gives an MSY value of about 8 500 t with an effort of 1 200 standard days. Assuming this result is valid, the fishery in the latest three years up to 1980 has been operating at an effort of 24 percent higher on average than that providing the MSY.

3. REFERENCES

Aoyama, T. and T.T. Nguyen, Stock assessment of cuttlefish off the coast of the People's
1979 Democratic Republic of Yemen. Tokyo, Ocean Research Institute, University of Tokyo, 36 p. (Unpubl.)

Beverton, R.J.H. and S.J. Holt, On the dynamics of exploited fish populations. Fish.
1957 Invest.Minist.Agric.Fish.Food G.B.(2 Sea Fish.), 19:533 p.

Castellanos, Z.A. and R. Menni, Nota preliminar sobre distribución de los cefalópodos del
1969 Atlántico Sudoccidental. Lista de especies incluyendo las del sector antártico. An.Soc.Cient.Argent., 188:205-21

Fishery Committee for the Eastern Central Atlantic (CECAF), Report of the second session
1975 on the Working Party on resource evaluation. Rome, 3-6 December, 1973. FAO Fish.Rep., (158):91 p. Issued also in French

__________, Report of the *Ad hoc* Working Group on the assessment of cephalopod stocks.
1978 CECAF/ECAF Ser., (78/11):149 p. Issued also in French

__________, Report of the fifth session of the Working Party on resource evaluation.
1981 Dakar, Senegal, 15-17 October, 1980. FAO Fish.Rep., (244):127 p. Issued also in French

Hatanaka, H., Studies on the fisheries biology of common octopus off the northwest coast
1979 of Africa. Bull.Far Seas Fish.Res.Lab., (17):13-124

Hempel, G., Area reviews on living resources of the ocean; Southwest Atlantic. FAO Fish.
1970 Tech.Pap., (97):176-85

Ikeda, I., Preliminary stock assessment of *Sepia* species off the coast of the People's
1975 Democratic Republic of Yemen. Far Seas Fisheries Research Laboratory, 3 p. (Unpubl. MS)

Japan Marine Fishery Resource Research Center, Fisheries survey report in the Argentine
1979 waters by R/V SHINKAI MARU. Tokyo, Japan Marine Fishery Resource Research Center, 133 p. (Unpubl.)

Kawahara, S. and K. Tokusa, Report on 1981 Japan/New Zealand joint squid survey in
1981 Areas E and F by SHINKAI MARU. Far Seas Fisheries Research Laboratory and JAMARC, 62 p. (Unpubl. MS)

Kawakami, T., Squid resources in the New Zealand waters. Tokai Regional Fisheries
1976 Research Laboratory, IPFC Doc., 13 p.

Mackett, D.J., Manual of methods for fisheries resource survey and appraisal, Part 3.
1973 Standard methods and techniques for demersal fisheries resource survey. FAO Fish.Tech.Pap., (124):39 p.

Pella, J.J. and P.K. Tomlinson, A generalized stock production model. Bull.I-ATTC,
1969 13:419-96

Pereiro, J.A. and J. Bravo de Laguna, Dinámica de la población y evaluación de los
1980 recursos del pulpo del Atlántico Centroriental. FAO Ser.CPACO/PACO, (80/18):63 p.

Sato, T., Tentative stock assessment of cuttlefish off the coast of the People's
1977 Democratic Republic of Yemen. Shimizu, Far Seas Fisheries Research Laboratory, 4 p. (Unpubl. MS)

Sissenwine, M.P. and A.M. Tibbetts, Simulating the effect of fishing on squid (*Loligo* and
1977 *Illex*) populations of the northeastern United States. Sel.Pap.ICNAF, 2:71-84

MESH SELECTION STUDY CONDUCTED IN THE PEOPLE'S DEMOCRATIC REPUBLIC OF YEMEN ON THE CUTTLEFISH *SEPIA PHARAONIS*

by

Michael J. Sanders and Mahmoud Bouhlel
Project for the Development of Fisheries
in the area of the Red Sea and Gulf of Aden
RAB/81/002, P.O. Box 2223, Cairo, Egypt

ABSTRACT

The results of codend mesh selection trials involving the alternate haul method are described. The mesh sizes used as determined by an ICES gauge were 6.5, 10.4, 12.4, 13.7, and 16.5 cm; the smallest size being taken as the standard. The codend material was single braided polyethylene. The relationship obtained between the 50 percent selection lengths and mesh sizes:

50 percent selection length (cm) = 2.03 x mesh size (cm) - 7.4

is shown to be highly significant.

RESUME

On trouvera décrits les résultats d'essais de sélection de mailles de cul de chalut comportant une nouvelle méthode de halage. La dimension des mailles utilisées, déterminée par un gabarit CIEM, était de 6,5, 10,4, 12,4, 13,7, et 16,5 cm, la plus petite taille servant d'étalon. Le cul de chalut est fabriqué en monofil de polyéthylène tressé. On peut constater que le rapport entre la sélectivité de 50 pour cent et le maillage:

sélectivité de 50 pour cent (en cm) = 2,03 x dimension de la maille (cm) - 7,4

est très significatif.

RESUMEN

Se describen los resultados de algunas pruebas de selección de la malla del copo, en las que se utilizó el método de arrastre alterno. Las mallas utilizadas, medidas con un calibrador del CIEM, tenían una luz de 6,5, 10,4, 12,4, 13,7 y 16,5 cm; la medida más pequeña se tomó como estándar. En los copos se empleó hilo trenzado sencillo de polietileno. La relación obtenida entre las tallas que arrojaban una selección del 50 por ciento y las luces de malla resultó muy significativa:

talla (cm) con selección del 50 por ciento = 2,03 x luz de malla (cm) - 7,4

INTRODUCTION

This paper describes the results of an ongoing study undertaken to determine the mesh selection properties of codends of various mesh sizes. The study is a joint activity involving the staffs of the UNDP/FAO Project RAB/81/002 (previously RAB/77/008) and the PDRY's Ministry of Fishwealth.

MATERIALS AND METHODS

The study has so far consisted of two trial periods for each of which the results have been analysed separately During the first period data were collected on each of seven days from 25 to 31 March 1981, while the second period included the collection of data for each of nine days between October and 10 November 1981.

The vessel used was the IBN MAGID, the PDRY Ministry of Fishwealth's 37.8 m (overall length) training and research vessel. The other specifications of the vessel are breadth 8 m (MLD), depth 3.8 m (MLD), draught 3 m (Designed), gross tonnage 250.31 t and main engine horse power 900 hp. The specifications of the trawl net and floats, otter boards and bridle attachments, are given in Figures 1, 2, and 3. The general fishing locations were adjacent to Ras Fartak, Thamnun, Thabut and Sayhul; see Figure 4.

The experimental design was based on the "alternate haul" method as described in Pope *et al.* (1975), with codends of the following five mesh sizes being available for comparison: 6.5 cm, 10.4 cm, 12.4 cm, 13.7 cm and 16.5 cm. Details of the design of each codend are given in Figure 5; all were made from single-braided polyethylene. Measurements of the meshes were done immediately after each use in an experimental haul, using an ICES gauge set at 5 kg pressure.

Generally three experimental hauls were conducted each day, with the time duration of each being mostly two hours. The order in which the codends were used during each day was random, except to minimize the number of codend changes the first codend used was the last of the previous day. The mantle lengths of all the cuttlefish caught were measured in the way depicted in Figure 6.

The data analysis involved combining for each codend separately, the cuttlefish length compositions resulting from each experimental haul. Determining the selection lengths for each "test" codend involved the application of the maximum likelihood method, as described in Pope *et al.* (1975). The 6.5 cm codend was chosen as the "standard", despite the complication caused by its loss during the second trial period.

For the period subsequent to its loss, the length frequency that "would" have been obtained from using the 6.5 cm codend, was estimated from the length frequency obtained when using the 10.4 cm codend. The estimation involved adjusting the numbers caught at each length with the 10.4 cm codend, according to the properties of the selection curve obtained when "comparing" this with the 6.5 cm codend during the March 1981 trial period.

The relationship between the 50 percent selection lengths and codend mesh sizes was investigated using the Hewlett Packard 97 Standard Pac Programme No.3. Separate analyses were undertaken in respect to the pairs of values from each trial period separately, and then combined. The effect of "weighting" the pairs of values, using the reciprocals of the variances of the 50 percent selection lengths as the weighting factors, was also examined.

RESULTS

A summary of the fishing locations, water depths, hauling speeds, sea conditions, codend identities, and catches for each experimental haul are given in Tables 1 and 2, while the results of the codend measurements taken are given in Tables 3 and 4. The length frequencies of the cuttlefish caught during each experimental haul are given in Tables 5 through 13. Plots of the length frequencies and the related selection curves are given in Figures 7 through 12. The estimated 50 percent selection lengths for each codend mesh size are shown plotted in Figure 13; the linear relationship depicted being for weighted value pairs in respect to both trial periods combined. The estimates for the 50 percent selection lengths, with confidence limits, and the selection ranges are given in Table 14. A summary of the results of the linear regression analyses of 50 percent selection lengths against codend mesh size are given in Table 15.

CONCLUSIONS AND DISCUSSION

An obvious conclusion is that the sizes of cuttlefish in the catches are able to be affected by the choice of codend mesh size, at least under the "ideal" conditions prevailing during the trial periods. Larger mesh sizes were associated with catches containing fewer small cuttlefish, as reflected by the 50 percent selection lengths increasing with increase in codend mesh size.

The assumed linear relationship between the 50 percent selection lengths and the codend mesh sizes was examined by applying a "t test" to the correlation coefficients as described in Bazigos (1974) and found to be significant, at $P<0.05$ when considering the values from the more recent trial period, at $P<0.10$ in respect to the values from the earlier trial, and at $P<0.01$ when considering the values from both trials combined.

In respect to determining whether the regression coefficients for the two trial periods were different, the "null hypothesis" that they were the same was tested as described in Bazigos (1974), and found not to be rejected at $P<0.05$. Similarly it was determined, that the regression coefficients obtained from the "unweighted" pairs were the same at $P<0.05$, when compared with those obtained when the pairs were weighted by the reciprocals of the variances of the 50 percent selection lengths.

The regression equation describing the relationship, after weighting the pairs is:

50 percent selection length (cm) = 2.03 x mesh size (cm) - 7.41.

This relationship provides a means of identifying the most appropriate codend size to adopt in order to achieve a given 50 percent selection length.

Concerning the individual selection lengths, those obtained relevant to the 12.4 cm mesh size were almost identical for each trial period. The 13.7 cm mesh size, which was also used on both occasions, gave substantially higher 50 percent selection length with lower confidence limits in respect to the second trial period. The values for the latter fit more closely with the relationship between the 50 percent selection lengths and mesh sizes as shown in Figure 13, and presumably are the more correct.

The selection range in respect to the 10.3 cm and 12.4 cm mesh sizes were found to be "reasonably narrow", and about half the selection ranges for the 13.7 cm and 16.8 cm codend. It is suspected that the higher selection ranges found for the latter reflects greater "experimental error", rather than the real situation.

REFERENCES

Bazigos, G.P., 1974 Applied fishery statistics. FAO Fish.Tech.Pap., (135):164 p. Issued also in French and Spanish.

Pope, J.A., *et al.*, 1975 Manual of methods for fish stock assessment. Part 3. Selectivity of fishing gear. FAO Fish.Tech.Pap., (41)Rev.1:65 p.

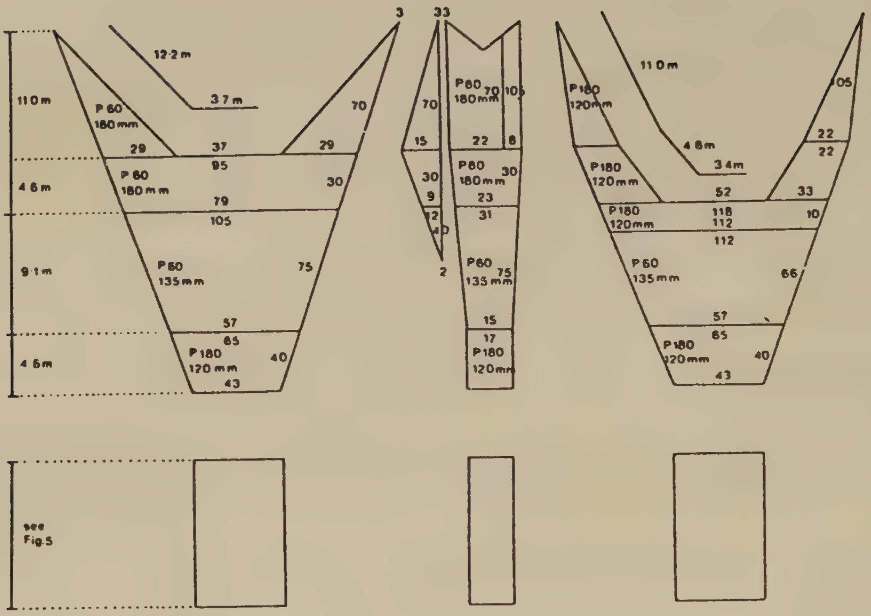

12·2 m
3 7 m
11 0 m
P 60
180 mm
29
37
29
70
4 6 m
95
P 60
180 mm
30
79
105
9·1 m
P 60
135 mm
75
57
65
4 6m
P 180
120 mm
40
43
3
33
70
15
30
9
12
40
2
P 60
180 mm
70
105
22
8
P 60
180 mm
30
23
31
P 60
135 mm
75
15
17
P 180
120 mm
11 0 m
P 180
120 mm
4 8m
3 4m
105
22
22
P 180
120 mm
52
33
P 180
120 mm
118
112
10
112
P 60
135 mm
66
57
65
P 180
120 mm
40
43
see
Fig.5

Figure 1 Net dimensions of the bottom trawl used during the study

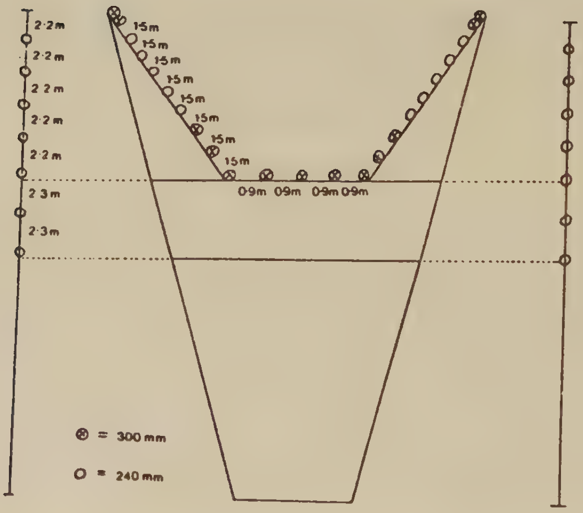

2·2 m
2·2 m
2 2 m
2·2 m
2·2 m
2 3 m
2·3 m
1·5 m
1·5 m
1·5 m
1·5 m
1·5 m
1·5 m
1·5 m
1·5 m
0·9 m
0·9 m
0·9 m
0·9 m
⊗ = 300 mm
○ = 240 mm

Figure 2 Diagram of the float attachments on the bottom trawl used

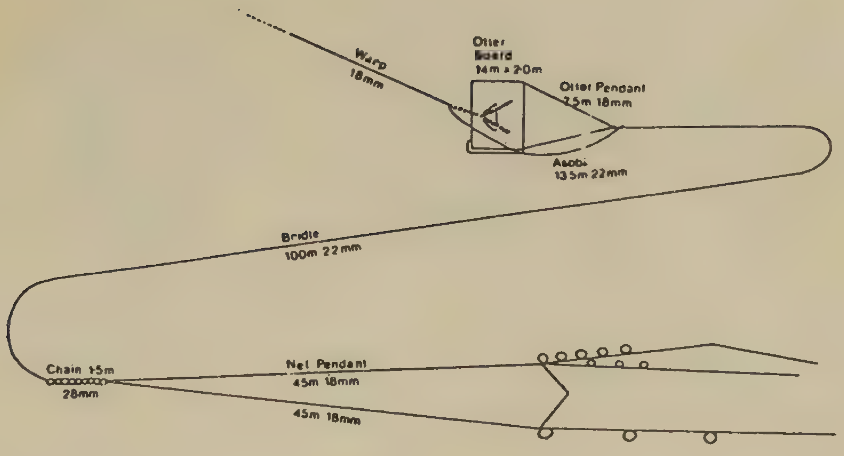

Warp
18mm
Otter
Board
1·4m x 2·0m
Otter Pendant
7·5m 18mm
Asobi
13·5m 22mm
Bridle
100m 22mm
Chain 1·5m
28mm
Net Pendant
45m 18mm
45m 18mm

Figure 3 Diagram of the otter board and bridle attachments on the bottom trawl used

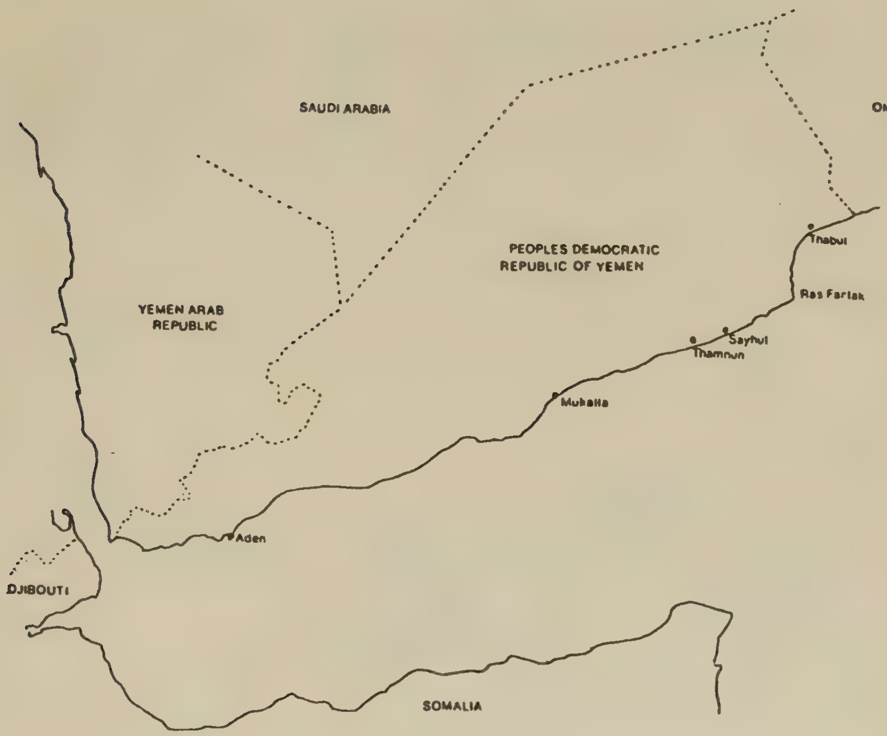

SAUDI ARABIA
OMAN
PEOPLES DEMOCRATIC REPUBLIC OF YEMEN
YEMEN ARAB REPUBLIC
Thabut
Ras Fartak
Sayhut
Thamnun
Mukalla
Aden
DJIBOUTI
SOMALIA

Figure 4 Diagram of the PDRY showing the locations of the Ras Fartak and Ras Darja.

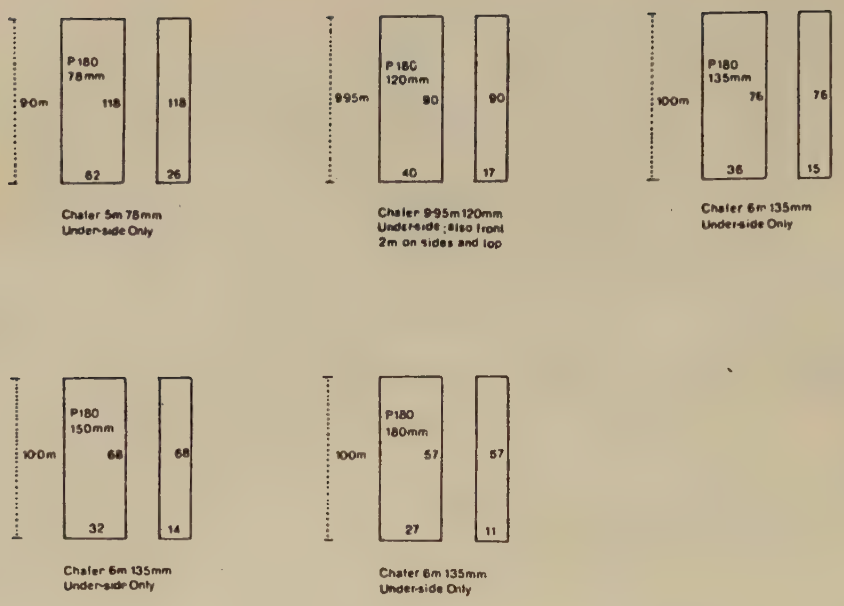

9·0m
P 180
78mm
118
118
62
26
Chaler 5m 78mm
Under-side Only
9·95m
P 180
120mm
90
90
40
17
Chaler 9·95m 120mm
Underside ; also front
2m on sides and top
10·0m
P 180
135mm
76
76
36
15
Chaler 6m 135mm
Under-side Only
10·0m
P180
150mm
68
68
32
14
Chaler 6m 135mm
Under-side Only
10·0m
P180
180mm
57
57
27
11
Chaler 6m 135mm
Under-side Only

Figure 5 Dimensions of the codends used during the study (note that "commercial" mesh size are given)

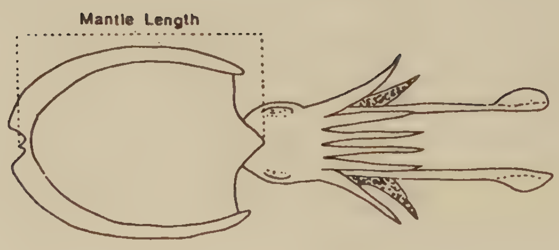

Mantle Length

Figure 6 Diagram depicting the mantle length measurements taken during the study.

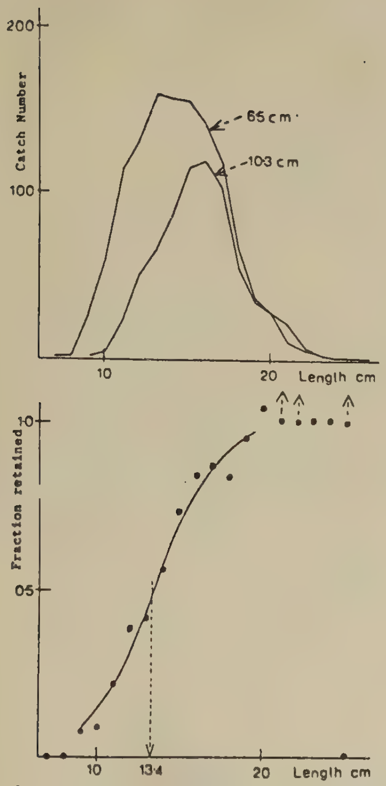


Figure 7 Length compositions and mesh selection curve for 10.3 cm codend; March 1981 trial

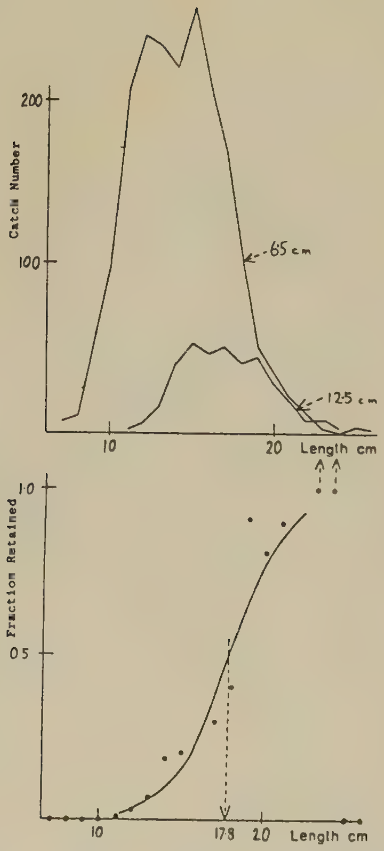


Figure 8 Length compositions and mesh selection curve for 12.5 cm codend; March 1981 trial

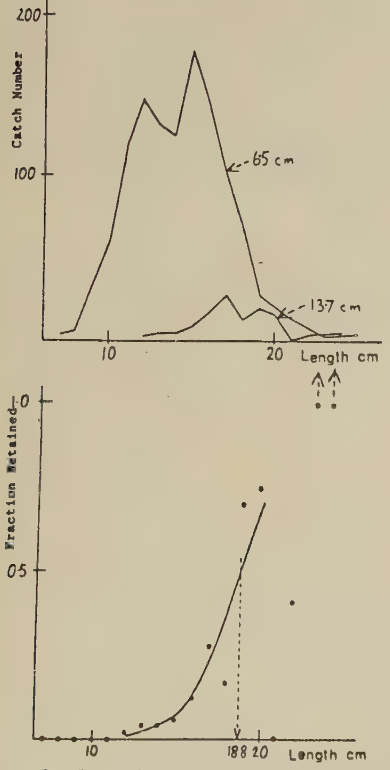


Figure 9 Length compositions and mesh selection curve for 13.7 cm codend; March 1981 trial

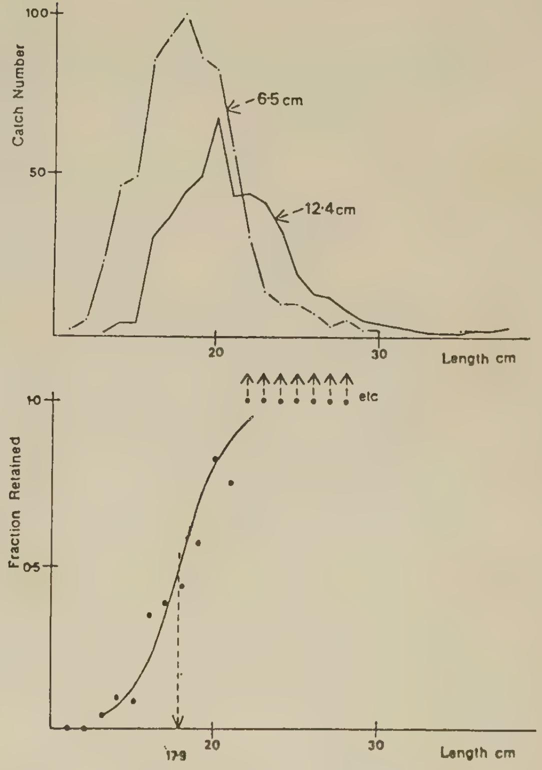


Figure 10 Length composition and mesh selection curve for 12.4 cm codend; Oct-Nov. 1981 trial

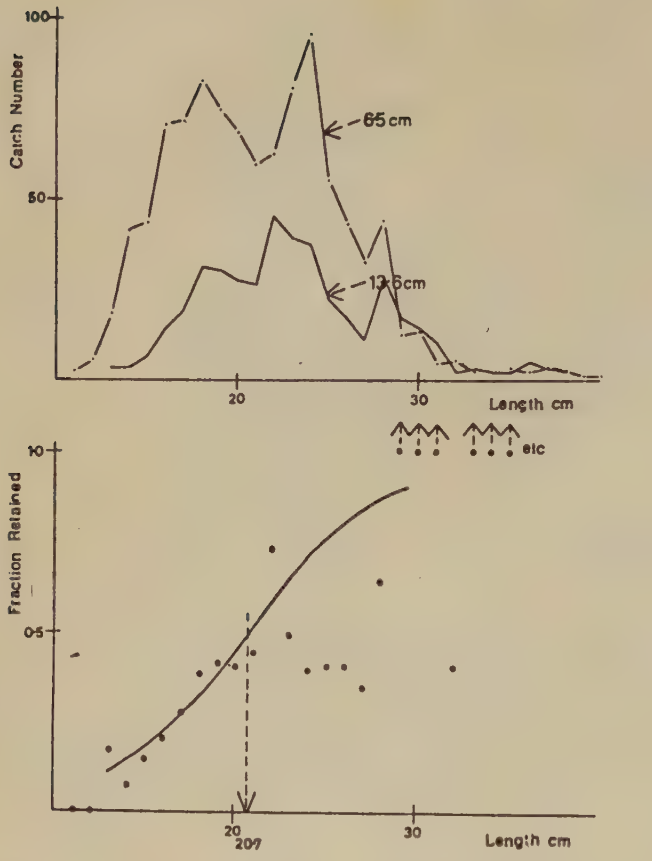


Figure 11 Length composition and mesh selection curve for 13.6 cm codend; Oct.-Nov. 1981 trial

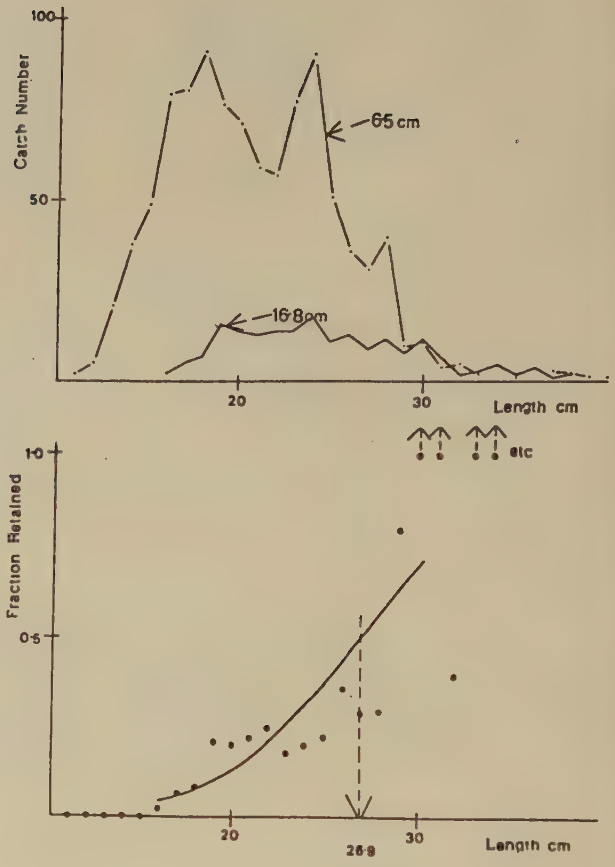


Figure 12 Length composition and mesh selection curve for 16.8 cm codend; Oct.-Nov. 1981 trial

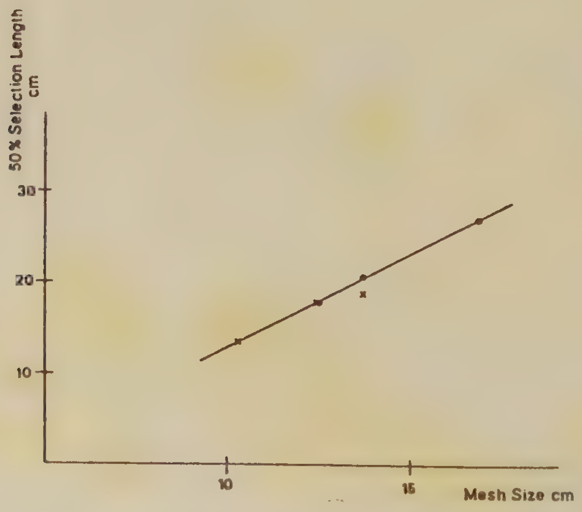


Figure 13 Plot of 50% selection lengths against mesh size; x from March 1981 trial and o from Oct.-Nov. 1981 trial

Table 1

Summary of fishing times and locations, vessel speeds, water depths, sea conditions, codend mesh sizes and catch weights for each experimental haul; March 1981 trial

Dates	Start Times	Stop Times	Haul Durations (hours)	Start Positions	Stop Positions	Vessel Speeds (n-miles)	Water Depths (metres)	Sea Conditions	Cod-end Mesh Sizes (mm)	Catch Weight All[a/] Species (Kg)
25.3.81	06.15	08.15	2	52°12.3'E 15°33.8'N	52°06.1'E 15°31.3'N	3.6	40	Calm	65	50
25.3.81	09.40	11.40	2	52°12.3'E 15°33.1'N	52°05.9'E 52°31.2'N	3.6	40	Calm	125	16
25.3.81	13.15	15.15	2	52°12.1'E 15°33.6'N	52°06.4'E 15°31.4'N	3.5	40	Calm	103	85
26.3.81	06.25	08.25	2	52°11.8'E 15°33.7'N	52°05.6'E 15°30.9'N	3.6	39	Calm	103	53
26.3.81	09.50	11.50	2	52°12.2'E 15°33.8'N	52°06.2'E 15°31.4'N	3.3	38	Calm	137	25
26.3.81	13.25	15.25	2	52°12.1'E 15°33.7'N	52°06.2'E 15°31.3'N	3.5	39	Calm	65	88
27.3.81	06.30	08.30	2	52°12.2'E 15°33.5'N	52°06.9'N 15°30.9'N	3.6	44	Slight	65	188
27.3.81	09.50	11.50	2	52°12.2'E 15°33.5'N	52°06.7'E 15°30.8'N	3.5	45	Slight	137	10
27.3.81	13.35	15.35	2	52°13.2'E 15°33.8'N	52°08.7'E 15°31.6'N	2.8	45	Slight	125	63
28.3.81	06.25	08.25	2	52°12.3'E 15°34.3'N	52°06.2'E 15°31.6'N	3.3	36	Calm	125	11
28.3.81	11.25	13.25	2	52°11.8'E 15°34.3'N	52°06.5'E 15°31.5'N	3.2	35	Calm	137	13
28.3.81	14.50	16.50	2	52°12.1'E 15°34.1'N	52°06.4'E 15°31.7'N	3.2	36	Calm	65	375
29.3.81	08.05	10.05	2	52°05.0'E 15°29.8'N	51°58.8'E 15°26.8'N	3.2	46	Calm	65	293
29.3.81	11.30	13.30	2	52°04.7'E 15°29.7'N	51°59.0'E 15°27.7'N	3.2	43	Calm	137	2
29.3.81	14.50	16.50	2	52°04.8'E 15°29.9'N	51°58.8'E 15°26.8'N	3.2	47	Calm	125	165
30.3.81	06.35	08.35	2	52°06.6'E 15°30.8'N	52°12.2'E 15°33.5'N	3.5	46	Calm	125	50
30.3.81	10.00	12.00	2	52°06.6'E 15°30.7'N	52°12.6'E 15°33.3'N	3.2	45	Calm	65	125
30.3.81	13.41	15.41	2	52°06.6'E 15°30.8'N	52°12.6'E 15°33.3'N	3.3	46	Calm	103	115
31.3.81	06.33	08.33	2	52°06.7'E 15°30.4'N	52°11.9'E 15°33.0'N	3.3	44	Calm	103	74
31.3.81	09.58	11.58	2	52°05.6'E 15°29.9'N	52°11.6'E 15°32.8'N	3.2	46	Calm	125	19
31.3.81	13.15	15.15	2	52°05.6'E 15°29.9'N	52°11.6'E 15°32.8'N	3.2	46	Calm	65	175

[a/] Refers to catches retained; which by eye-estimate were about 15-20 percent of the total; except for the third haul on the 27.3.1981 when about 5 t of the catfish *Arius thalassinus* were discarded, and the second haul on the 29.3.1981 when about 3 t of catfish were discarded

Table 2

Summary of fishing times and locations, vessel speeds, water depths, sea conditions, codend mesh sizes and catch weights for each experimental haul; Oct.-Nov. 1981 trial.

Dates	Start times	Stop times	Haul Durations (hours)	Start Positions	Stop Positions	Vessel Speeds (n-miles)	Water Depths (metres)	Sea Condition	Cod-end mesh sizes(cm)	Approx.Catch weight (all species) (kg)
2.10.81	08.47	09.47	1	50° 52.2'E 15° 01.9'N	50° 54.9'E 15° 01.9'N	3.4	40	Calm	6.6	172
2.10.81	11.28	12.28	1	50° 51.6'E 15° 01.9'N	50° 55.4'E 15° 02.5'N	3.6	40	Calm	13.6	24
2.10.81	13.52	14.52	1	50° 52.2'E 15° 01.9'N	50° 55.9'E 15° 02.5'N	3.3	39	Calm	16.8	20
2.10.81	16.03	17.03	1	50° 52.7'E 15° 01.9'N	50° 55.6'E 15° 02.3'N	3.3	39	Calm	12.4	30
3.10.81	06.53	08.53	2	50° 52.0'E 15° 01.9'N	50° 59.3'E 15° 02.7'N	3.4	39	Calm	12.4	55
3.10.81	10.43	12.43	2	50° 51.8'E 15° 01.7'N	50° 59.2'E 15° 02.5'N	3.4	41	Calm	6.6	70
3.10.81	14.30	16.30	2	50° 51.8'E 15° 01.7'N	50° 59.8'E 15° 02.6'N	3.4	39	Calm	13.6	2
30.10.81	06.45	08.45	2	52° 21.6'E 16° 10.1'N	52° 24.5'E 16° 16.4'N	3.6	20	Calm	10.4	69
30.10.81	09.59	11.59	2	52° 21.8'E 16° 10 8'N	52° 25.1'E 16° 17.2'N	3.6	20	Calm	12.4	158
30.10.81	13.30	15.30	2	52° 21.5'E 16° 10.5'N	52° 24.7'E 16° 16.3'N	3.6	19	Calm	13.6	41
31.10.81	07.10	09.10	2	52° 21.3'E 16° 09.7'N	52° 24.5'E 16° 15.7'N	3.6	21	Calm	13.6	292
31.10.81	10.38	12.38	2	52° 21.3'E 16° 09.5'N	52° 24.3'E 16° 15.5'N	3.6	20	Calm	10.4	494
31.10.81	14.00	16.00	2	52° 21.2'E 16° 09.1'N	52° 24.3'E 16° 14.9'N	3.6	20	Calm	16.8	183
6.11.81	06.30	08.30	2	51° 12.7'E 15° 07.6'N	51° 19.4'E 15° 09.5'N	3.5	23	Calm	10.4	29
6.11.81	09.58	11.58	2	51° 13.1'E 15° 07.7'N	51° 19.9'E 15° 09.7'N	3.6	21	Calm	13.6	39
6.11.81	13.09	15.09	2	51° 13.1'E 15° 07.6'N	51° 19.9'E 15° 10.3'N	3.6	22	Calm	12.4	57
6.11.81	16.17	18.17	2	51° 14.7'E 15° 08.2'N	51° 21.2'E 15° 10.7'N	3.6	20	Calm	16.8	32
7.11.81	07.25	09.25	2	51° 14.3'E 15° 07.9'N	51° 21.4'E 15° 10.4'N	3.6	22	Calm	16.8	18
7.11.81	10.48	12.48	2	51° 12.4'E 15° 07.6'N	51° 22.3'E 15° 10.4'N	3.4	21	Calm	10.4	68
7.11.81	13.57	15.57	2	51° 13.7'E 15° 07.9'N	51° 20.7'E 15° 10.2'N	3.5	20	Calm	12.4	38
8.11.81	08.22	10.22	2	51° 12.9'E 15° 02.3'N	51° 20.2'E 15° 10.1'N	3.6	21	Calm	12.4	43
8.11.81	11.40	13.40	2	51° 12.8'E 15° 07.6'N	51° 19.8'E 15° 09.7'N	3.6	23	Calm	13.6	37
8.11.81	14.50	16.50	2	51° 12.6'E 15° 07.8'N	51° 19.4'E 15° 09.6'N	3.6	21	Calm	10.4	40
9.11.81	06.41	08.41	2	51° 13.1'E 15° 07.9'N	51° 20.3'E 15° 10.3'N	3.6	20	Calm	10.4	24
9.11.81	09.54	11.54	2	51° 13.7'E 15° 07.8'N	51° 20.7'E 15° 10.3'N	3.6	20	Calm	16.8	24
9.11.81	13.14	15.14	2	51° 13.9'E 15° 07.9'N	51° 20.8'E 15° 09.9'N	3.6	23	Calm	13.6	31
10.11.81	10.18	12.18	2	51° 12.0'E 15° 06.0'N	51° 19.0'E 15° 07.5'N	3.6	40	Calm	10.4	52
10.11.81	13.23	15.23	2	51° 13.7'E 15° 06.0'N	51° 20.3'E 15° 07.6'N	3.6	40	Calm	16.8	-

Table 3

Codend mesh measurements; March 1981 trial

Mean Mesh Opening	65.94	64.86	66.03	63.92	65.14	65.14	65.17	64.56	64.97
Standard Deviation	2.38	2.61	2.01	1.63	1.79	2.38	2.60	2.84	2.36
Range	61-71	59-72	63-71	61-68	61-69	60-69	59-73	55-68	55-73
Sample Number	36	36	36	36	36	36	36	36	252
Measured Wet or dry	Dry	Wet	Wet	Wet	Wet	Wet	Wet	Wet	Wet
Measurement Date	20.3.81	25.3.89	26.3.81	27.3.81	28.3.81	29.3.81	30.3.81	31.3.81	(total)
Mean Mesh Opening	101.11	101.44	102.72	Not Used	Not Used	Not Used	103.03	103.75	102.74
Standard Deviation	2.30	2.12	2.04				3.00	2.69	2.60
Range	94-105	98-106	98-110				95-111	97-109	95-111
Sample Number	36	36	36				36	36	144
Measured Wet or Dry	Dry	Wet	Wet				Wet	Wet	Wet
Measurement Date	20.3.81	25.3.81	26.3.81				30.3.81	31.3.81	(total)
Mean Mesh Opening	121.30	124.31	Not Used	125.33	124.47	124.58	123.72	125.11	124.60
Standard Deviation	4.15	3.86		3.30	3.53	5.04	4.48	4.48	4.15
Range	110-129	116-132		118-131	119-133	115-135	115-137	117-134	115-137
Sample Number	36	36		36	36	36	36	36	216
Measured Wet or Dry	Dry	Wet		Wet	Wet	Wet	Wet	Wet	Wet
Measurement Date	20.3.81	25.3.81		27.3.81	28.3.81	29.3.81	30.3.81	31.3.81	(total)
Mean Mesh Opening	137.31	Not Used	137.08	135.86	137.03	136.53	Not Used	Not Used	136.60
Standard Deviation	2.67		1.93	4. 22	1.50	2.24			2.69
Range	131-142		133-142	127-153	134-140	131-143			127-153
Sample Number	36		36	36	36	36			144
Measured Wet or Dry	Dry		Wet	Wet	Wet	Wet			Wet
Measurement Date	20.3.81		26.3.81	27.3.81	28.3.81	29.3.81			(total)
Mean Mesh Opening	165.50	Not Used	Not Used	Not Used	Not Used	Not Used	Not Used	Not Used	Not Used
Standard Deviation	5.57								
Range	151-174								
Sample Number	36								
Measured Wet or Dry	Dry								
Measured Date	20.3.81								

Table 4

Codend mesh measurements, October-November 1981 trial

Mean Mesh Opening(cm)	6.42	6.52	6.71	Not available	Not available	Not available	Not available	Not available	Not available	Not available	Not available	6.57
Standard Deviation	0.26	0.29	0.22									
Range (cm)	6.1 - 7.1	5.7 - 7.1	6.3 - 7.1									5.7 - 7.1
Sample Number	36	36	36									72
Measured Wet or dry	Dry	Wet	Wet									Wet
Measurement Date	26.9.81	2.10.81	3.10.81									(total)
Mean Mesh Opening(cm)	Not measured	Not used	Not used	10.36	10.38	10.37	10.41	10.49	10.32	10.44	10.43	10.40
Standard Deviation				0.22	0.20	0.31	0.26	0.18	0.22	0.33	0.22	
Range (cm)				9.8 -10.9	9.7 -10.7	9.7 -11.3	9.8 -11.0	10.1-10.8	9.8 -10.7	9.6-10.9	10.0-10.8	9.5-11.3
Sample Number				36	36	36	36	36	36	36	36	252
Measured Wet or Dry				Dry	Wet	Wet	Wet	Wet	Wet	Wet	Wet	Wet
Measurement dat.				22.10.81	30.10.81	31.10.81	6.11.81	7.11.81	8.11.81	9.11.81	10.11.81	(total)
Mean Mesh Opening(cm)	12.23	12.29	12.43	12.13	12.26	Not used	12.32	12.36	12.48	Not used	Not used	12.36
Standard Deviation	0.405	0.46	0.465	0.45	0.39		0.39	0.51	0.46			
Range (cm)	11.4-13.2	11.5-13.3	11.4-13.6	11.3-12.7	11.6-13.1		11.3-13.3	11.3-13.4	11.5-13.3			11.3-13.6
Sample Number	36	36	36	36	36		36	36	36			216
Measured Wet or Dry	Dry	Wet	Wet	Dry	Wet		Wet	Wet	Wet			Wet
Measurement Date	26.9.81	2.10.81	3.10.81	22.10.81	30.10.81		6.11.81	7.11.81	8.11.81			(total)
Mean Mesh Opening(cm)	13.49	13.64	13.65	13.43	13.66	13.59	13.60	Not used	13.6	13.65	Not used	13.63
Standard Deviation	0.23	0.26	0.21	0.245	0.31	0.46	0.26		0.26	0.23		
Range (cm)	12.9-14.0	13.0-14.0	13.2-14.1	13.0-13.9	12.6-14.3	12.3-14.7	13.2-14.2		12.9-14.0	13.3-14.2		12.3-14.7
Sample Number	36	36	36	36	36	36	36		36	36		252
Measured Wet or Dry	Dry	Wet	Wet	Dry	Wet	Wet	Wet		Wet	Wet		Wet
Measurement Date	26.9.81	2.10.81	3.10.81	22.10.81	30.10.81	31.10.81	6.11.81		8.11.81	9.11.81		(total)
Mean Mesh Opening(cm)	16.83	16.94	Not used	16.60	Not used	16.69	16.70	16.99	Not used	16.88	16.82	16.84
Standard Deviation	0.48	0.51		0.49		0.48	0.71	0.52		0.42	0.66	
Range (cm)	15.6-17.6	15.8-17.7		15.8-17.5		15.7-17.8	14.8-17.5	15.1-17.5		16.1-17.5	15.0-17.7	14.8-17.8
Sample Number	36	36		36		36	36	36		36	36	216
Measured Wet or Dry	Dry	Wet		Dry		Wet	Wet	Wet		Wet	Wet	Wet
Measurement Date	26.9.81	2.10.81		22.10.81		31.10.81	6.11.81	7.11.81		9.11.81	10.11.81	(total)

Table 5

Number of cuttlefish by length taken during each experimental haul with the 6.5 cm codend, March 1981 trial

Mantle lengths (cm)	Numbers of cuttlefish of each length taken on the following dates						
	25.3.81	26.3.81	27.3.81	28.3.81	29.3.81	30.3.81	31.3.81
7			5			1	1
8			2	5		3	
9		4	24	5	1	19	6
10	1	11	37	11	3	24	25
11	13	12	76	19	8	50	39
12	9	20	92	18	16	54	50
13	13	28	73	20	9	60	59
14	18	31	51	28	13	58	51
15	17	37	87	39	13	49	53
16	32	39	62	30	10	43	29
17	28	25	44	23	8	37	29
18	11	15	30	16	6	21	19
19	7	6	13	4	3	10	14
20	8	5	11	2	1	7	8
21	3	1	8	2	1	5	2
22	2		3	1	1	3	1
23	1	1				1	
24		1					
25			1	1			1
26						1	
27							
28							
29							
30							
31							
32							
TOTAL	163	236	619	224	93	446	387

Table 6

Number of cuttlefish by length taken during each experimental haul with the 10.3 cm codend; March 1981 trial

Mantle lengths (cm)	Numbers of cuttlefish of each length taken on the following dates						
	25.3.81	26.3.81	27.3.81	28.3.81	29.3.81	30.3.81	31.3.81
7							
8							
9	2						
10						3	2
11	4	1				15	4
12	10	1				29	10
13	8	5				45	7
14	16	21	Not used	Not used	Not used	33	18
15	27	15				65	9
16	28	20				54	18
17	32	10				48	13
18	13	11				25	6
19	8	6				15	6
20	6	3				17	3
21	7	3				8	4
22	1	2				2	4
23	1					2	
24		1					
25							
26		1	Not used	Not used	Not used		
27							
28							
29							
30							
Total	163	100				362	104

Table 7

Numbers of cuttlefish by length taken during each experimental haul with the 12.5 cm codend; March 1981 trial.

Mantle lengths (cm)	Numbers of cuttlefish of each length taken on the following dates						
	25.3.81	26.3.81	27.3.81	28.3.81	29.3.81	30.3.81	31.3.81
7							
8							
9							
10				a/			
11			1	1			
12	2		1	1		2	
13		Not used	4	5	1	4	2
14	3		10	13	3	7	5
15	5		14	18	6	5	5
16	8		10	13	1	9	6
17	11		7	9	4	14	6
18	10		7	9	3	9	4
19	9		9	11	4	7	7
20	2		10	13	1	2	2
21	3		2	3	2	6	3
22	2				3		1
23			1	1	2	3	
24		Not used			1	1	
25							
26							
27							
28							
29							
30							
TOTALS	55		76	97	31	69	41

a/ Adjusted numbers, raised by multiplying by 1.26 to account for the reduced distance travelled

Table 8

Numbers of cuttlefish by length taken during each experimental haul with the 13.7 cm codend; March 1981 trial.

Mantle lengths (cm)	Numbers of cuttlefish of each length taken on the following dates						
	25.3.81	26.3.81	27.3.81	28.3.81	29.3.81	30.3.81	31.3.81
7							
8							
9							
10							
11							
12	Not used			3		Not used	Not used
13			1	4			
14		3		2			
15		3	1	5			
16		6	3	8			
17		4	7	13	3		
18		4	1	5	1		
19		7	6	4	1		
20		2	5	5	2		
21							
22			2				
23		1	1				
24		2	1				
25	Not used					Not used	Not used
26							
27							
28							
29							
30							
31							
32							
33					1		
TOTALS		32	28	49	8		

Table 9

Number of cuttlefish by length taken during each experimental haul with the 6.5 cm codend; October-November 1981 trial

Mantle lengths (cm)	Numbers of Cuttlefish of each length, taken on the following dates								
	2.10.81	3.10.81	30.10.81	31.10.81	6.11.81	7.11.81	8.11.81	9.11.81	10.11.81
11	2		Not used	Not used	Not used	Not used	Not used	Not used	Not used
12	2								
13	14								
14	31	3							
15	32	1							
16	55	1							
17	55	1							
18	56	4							
19	40	2							
20	33	4							
21	33	3							
22	15	4							
23	11	2							
24	4								
25	4								
26									
27	2								
28									
Total	389	25							

Table 10

Numbers of cuttlefish by length taken during each experimental haul with the 10.4 cm codend; October-November 1981 trial

Mantle lengths (cm)	Numbers of Cuttlefish of each length, taken on the following dates								
	2.10.81	3.10.81	30.10.81	31.10.81	6.11.81	7.11.81	8.11.81	9.11.81	10.11.81
12					1				
13					1	2	1		
14					1	3	3		
15					4	6	1	2	
16					3	13	6	2	1
17					4	18	9		
18					11	18	7	2	1
19			1	2	9	18	13	5	
20			2	5	5	22	14	4	1
21			3	8	4	9	4	4	
22			2	35	3	3	3		1
23			1	65				1	
24			5	83	1			2	
25			5	46		1			
26	Not Used	Not Used	6	36			26		
27			1	28				1	
28			4	39	1				
29			2	10					
30			2	11					
31				4					
32				5					
33				2					
34									
35			2	1					
36			2						
37				3					
38				2					
39				1					
Total			38	386	48	113	62	23	4

Table 11

Numbers of cuttlefish by length taken during each
experimental haul with the 12.4 cm codend;
October-November 1981 trial

Mantle lengths (cm)	Numbers of Cuttlefish of each length taken on the following dates								
	2.10.81	3.10.81	30.10.81	31.10.81	6.11.81	7.11.81	8.11.81	9.11.81	10.11.81
13					1				
14		2			1	1			
15					3	1			
16	9	10			5	6			
17	7	10	1		9	4	5		
18	2	11			19	6	6		
19	14	8	1		13	8	5		
20	13	19	1		15	13	6		
21	8	14	6		9	3	3		
22	3	12	14		6	5	4		
23	4	5	24		4	3	1		
24	3	3	23		1	1	1		
25		1	17	Not Used		1			
26		1	12					Not Used	Not Used
27			12						
28			8						
29			5						
30			4						
31			2		1				
32			2						
33			1						
34			1						
35			1						
36			2						
37			2						
38			3						
Total	63	96	142	-	87	52	31	-	-

Table 12

Numbers of cuttlefish by length taken during each experimental haul with the 13.6 cm codend; October-November 1981

Mantle lengths (cm)	Number of Cuttlefish of each length taken on the following dates								
	2.10.81	3.10.81	30.10.81	31.10.81	6.11.81	7.11.81	8.11.81	9.11.81	10.11.81
13	1				1		1		
14					2		1		
15		1			3		1	1	
16	9				2		3		
17	5	2			7		3	2	
18	12	2			9		7	1	
19	13	2		1	8		3	3	
20	4	1		1	10		6	5	
21	10		3	5	4		2	2	
22	11		8	17	1		5	3	
23	1		8	21	4		3	2	
24	1		5	26	2		3		
25			6	14			2		
26	1		1	14			1		
27				9		Not Used	2		Not Used
28			5	22			1		
29			1	16					
30				14					
31				10					
32				2					
33				2	1				
34				2					
35				2					
36				5					
37				3					
38				2					
39									
40				1					
Totals	68	8	37	189	54	-	44	19	

Table 13

Numbers of cuttlefish by length taken during each experimental haul with the 16.8 cm codend; October-November 1981

Mantle lengths (cm)	Numbers of Cuttlefish of each length taken on the following dates								
	2.10.81	3.10.81	30.10.81	31.10.81	6.11.81	7.11.81	8.11.81	9.11.81	10.11.81
16	1	Not Used	Not Used			1	Not Used		
17	2				2	1			
18	1				3	1		2	
19	3				9	2		2	
20	4				7	2		1	
21	5			3	3	2			
22	4			5	2	2		1	
23	1			11	2				
24	4			12		1		1	
25	1			10					
26				10	1	1			1
27				9					
28				10	2				
29				8					
30				12					
31				7					
32				2					
33				2	1				
34				5					
35				2					
36				4					
37				1					
38				2					
39									
40				1					
Totals	26	–	–	116	32	13	–	7	1

Table 14

Selection lengths and selection ranges when "comparing" the 10.3 cm, 12.4 cm, 13.6 cm and 16.8 cm codends, with the 6.5 cm codend

March 1981 Trial	Mesh Sizes (cm)	10.2 (7)	12.4 (6)	13.6 (6)	
	50% Selection Lengths with 95% confidence limits (cm)	13.42 ± 0.27	17.76 ± 0.45	18.80 ± 0.81	
	Selection Ranges 25% to 75% (cm)	11.37 - 15.47	15.84 - 19.68	17.14 - 20.46	
September-November 1981 Trial	Mesh Sizes (cm)		12.3 (6)	13.6 (3)	16.8 (4)
	50% Selection Lengths with 95% confidence limits (cm)		17.8(7)±0.2(8)	20.7(4)±0.5(3)	26.9(5)±1.0(7)
	Selection Ranges 35% to 75% (cm)		16.2(3)-19.5(2)	16.6(6)-24.8(3)	22.9(1)-30.9(9)

Table 15

Summary of linear regression analyses of 50 percent lengths against codend mesh size

Identification	March 1981 Trial		October to November 1981 Trial		March and October to November 81 trials combined	
	unweighted	weighted	unweighted	weighted	unweighted	weighted
y intercept, a	- 3.18	- 4.89	- 6.83	- 7.66	- 7.62	- 7.41
slope, b	1.64	1.79	2.01	2.07	2.04	2.03
regression coefficient, r	0.98*	0.98*	1.00**	1.00**	0.99***	0.99***
no. of input pairs, n	3	3	3	3	6	6
Est. 50% selection length when mesh size =						
10 (cm)	13.2	13.0	(13.3)	(13.0)	12.7	12.9
11	14.8	14.8	(15.3)	(15.1)	14.8	14.9
12	16.5	16.6	17.3	17.2	16.8	17.0
13	18.1	18.4	19.3	19.2	18.8	19.0
14	19.7	20.1	21.3	21.3	20.9	21.0
15	(21.4)	(21.9)	23.3	23.4	22.9	23.1
16	(23.0)	(23.7)	25.3	25.4	25.0	25.1
17	(24.6)	(25.5)	27.3	27.5	27.0	27.1

BIOLOGY OF THE CUTTLEFISH *SEPIA OFFICINALIS HIERREDDA* OFF THE SENEGALESE COAST

by

M. Bakhayokho
c/o CECAF
Development of Fisheries in
the Eastern Central Atlantic
c/o UNDP
P.O. Box 154
Dakar, Senegal

ABSTRACT

The distribution, reproduction and growth of *Sepia officinalis hierredda* were studied off Senegal.

Cuttlefish are caught at depths down to 120 m on the continental shelf, mainly south of the Cape Verde peninsula. Two migration cycles were observed, following major movements of water masses. The first one involved small and large specimens caught in the cold waters off Cape Verde in January, and off Sangomar and probably Casamance in March-June, before they return north in the warm tropical water masses. The second migration involves small and medium-sized cuttlefish that are caught off Pointe Sarène in July and off Sangomar in September, after which they were lost sight of. Other concentrations of this species appear to originate from Guinea Bissau waters in March, reach Casamance in May and return in July.

Coastward spawning migrations were also observed. Females mature at 13 cm mantle length. All sizes of adults spawn intensively from February through June, the largest ones first. One year old adults spawn from August to September. Each cuttlefish is thought to spawn once a year off Joal and Sangomar or off the Casamance estuary.

Total individual fecundity ranges from 250 eggs at 13 cm to 1 400 eggs at 35 cm mantle length. A preliminary growth analysis of males, using the Petersen method, indicates a growth rate of 2.6 cm per month up to a length of 10 cm, slowing down to 2.1 cm between 10 and 25 cm.

The longevity of *S. officinalis hierredda* seems to be at least two years.

RESUME

La distribution, la reproduction et la croissance de *Sepia officinalis hierredda* ont été étudiées au large des côtes du Sénégal.

Les seiches sont capturées à une profondeur de 120 m sur le plateau continental, essentiellement au sud de la Péninsule du Cap-Vert. On a remarqué deux cycles de migration, à la suite de déplacements importants de masses d'eau. Le premier concerne les petits et les grands spécimens capturés dans les eaux froides au large du Cap-Vert en janvier et au large de Sangomar et probablement de l'estuaire

de la Casamance en mars-juin, avant qu'ils ne regagnent les eaux chaudes tropicales du nord. La seconde migration intéresse les seiches de petites et moyennes dimensions qui sont capturées au large de Pointe Sarène en juillet et de Sangomar en septembre, après quoi, on les perd de vue. D'autres bancs de cette espèce semblent provenir des eaux de la Guinée-Bissau en mars, atteindre la Casamance en mai et revenir en juillet.

On a également remarqué des migrations côtières au moment du frai. Les femelles atteignent l'âge adulte lorsque la longueur du manteau est de 13 cm. Les adultes de toutes tailles frayent intensivement entre février et juin, les plus gros commençant les premiers. Les adultes d'un an frayent d'août à septembre. On pense que chaque seiche dépose des oeufs une fois par an au large de Joal et de Sangomar ou dans l'estuaire de la Casamance.

Le taux de fécondité individuel oscille entre 250 oeufs (manteau de 13 cm) à 1 400 oeufs (manteau de 35 cm). Une analyse préliminaire de la croissance des mâles, suivant la méthode de Petersen, indique un taux de croissance de 2,6 cm par mois jusqu'à 10 cm, puis de 2,1 cm entre 10 et 25 cm.

La durée de vie de *S. officinalis hierredda* semble être d'au moins deux ans.

RESUMEN

La distribución, reproducción y crecimiento del *Sepia officinalis hierredda* se estudiaron frente a las costas del Senegal.

La sepia se captura en la plataforma continental a profundidades de 120 m principalmente al sur de la península de Cabo Verde. Se observaron dos ciclos migratorios como consecuencia de importantes movimientos de las masas de aguas. El primero incluía ejemplares pequeños y grandes capturados en las aguas frías frente a la costa de Cabo Verde en enero y de Sangomar y probablemente Casamance en marzo y junio, antes de su regreso al norte en las masas de agua cálida tropical. La segunda migración incluye sepias de tamaño pequeño y mediano, capturadas frente a Pointe Sarène en julio y frente a Sangomar en septiembre, después de lo cual se perdieron de vista. Otras concentraciones de esta especie parecen tener su origen en aguas de Guinea-Bissau en marzo, llegando a Casamance en mayo para regresar en julio.

También se observaron emigraciones de desove hacia la costa. Las hembras maduran a los 13 cm de longitud del manto. Los adultos de todo tamaño desovan intensamente de febrero a junio, los más grandes primero. Los adultos de un año de edad desovan de agosto a septiembre. Se cree que cada sepia desova una vez al año frente a las costas de Joal y Sangomar o frente al estuario de Casamance.

La fecundidad individual total varía de 250 huevos, con una longitud de manto de 13 cm, a 1 400 huevos con 35 cm de longitud de manto. Un análisis preliminar del crecimiento de los machos, utilizando el método de Petersen, indica un índice de crecimiento de 2,6 cm por mes hasta una longitud de 10 cm, disminuyendo a 2,1 cm entre 10 y 25 cm.

La longevidad del *S. officinalis hierredda* parece ser de 2 años por lo menos.

INTRODUCTION

The cuttlefish, *Sepia officinalis hierredda* is a much sought after species off the coast of Senegal, with catches amounting to approximately 2 500 t per year, constituting 95 percent of the national cephalopod catches, for a value of approximately CFAF one thousand million. Rational management of this species should be based on the knowledge of its distribution, reproduction and growth. First we wish to identify the taxonomic position of this mollusc, and distinguish it from the other Sepiidae of the Senegalese and other African coasts.

1. IDENTITY AND TAXONOMIC STATUS OF WEST AFRICAN CUTTLEFISH SPECIES

1.1 Taxonomy of *Sepia officinalis hierredda*, Rang 1837

Class	Cephalopoda, Cuvier 1798
Subclass	Coleoidea (Dibranchiata), Bather 1888
Order	Decapoda
Suborder	Sepiodea, Naef 1961
Family	Sepiidae, Linne 1758
Genus	*Sepia*
Species	*officinalis*
Subspecies	*hierredda*

1.1.1 Identification

Rang (1837) and Adam (1941) have given a complete description of *Sepia officinalis hierredda*; Rang 1837, to which we refer for a detailed diagnosis. Since a number of other cuttlefish are frequently found in landings (*Sepia bertheloti*, *Sepia orbignyana*, *Sepia elobyana*, *Sepiella ornata*) or are reported in the region (*Sepia officinalis officinalis* and *Sepia officinalis vermiculata*), it is useful to describe their distinctive characters. Table 1, based on the FAO species identification sheets for the CECAF area (1982) summarizes the characters distinguishing the *Sepia* spp. and *Sepiella ornata* of northwest Africa. Besides *S. officinalis officinalis* and *S. officinalis hierredda*, a third subspecies *S. officinalis vermiculata* was described by Adam (1941), but it is not mentioned in the identification sheets. As Adam stressed that additional data were needed for the distinction of the subspecies, it was decided to undertake a biometric study of the *S. officinalis hierredda* off the Senegalese coast. The results of this study will be discussed in a later section.

2. MEANS AND METHODS OF OBTAINING DATA

The data used to study the distribution, reproduction and growth of *S. officinalis hierredda* come from two sources: biological sampling and catch statistics.

2.1 Biological Sampling

2.1.1 Research vessel

The biological samples were obtained from the centre's oceanographic research vessel, R/V LAURENT AMARO. This vessel is a 24-m long and 380-hp propulsion seiner/trawler, equipped with a Le Drezen trawl of 24 m headline and a mesh size of 25 mm in the codend. Two otter boards of 250 kg each provide the trawl opening and allow it to be used for bottom, as well as pelagic trawling. As the gear is not specially suited for the cephalopod fishery, the trawling data from this vessel will be used only for reproduction studies. Trawling stations, determined according to the nature of the grounds and the depth (Figure 1) were surveyed every month from April to October 1979. During the other months the boat was unavailable except in March 1980, when a trip was made off northern Senegal. The duration of the hauls averaged 30 min, at an average speed of 3.5 kn. Cuttlefish were relatively uncommon. At each station, the specimens caught were identified, sorted, measured individually (nearest cm) and weighed (nearest 100 g), after which the stage of sexual maturation was determined and the cuttlefish were kept in cold storage for further study at the laboratory.

Table 1

	S. officinalis officinalis	*S. officinalis hierredda*	*S. bertheloti*	*S. elegans*	*S. elobyana*	*S. orbignyana*	*Sepiella ornata*
max. size, cm (dorsal mantle)	40 cm (= 3.5 kg)		♀13 ♂17.5	9		12	10
Hectocotyles (left ventral arm)	Proximal 5-8 horizontal rows of suckers reduced in size	Proximal 8-13 horizontal rows of suckers reduced in size	2-5 normal suckers at base, and 9-13 rows of minute spaced suckers on proximal third	Two-thirds of length hectocotylized, very few normal basal suckers, followed by 9-11 rows of minute, widely spaced suckers arranged in zig-zag pattern. Distal third with oblique rows of normal suckers	Basal two-fifths of arms with greatly reduced suckers	Proximal dorsal and ventral suckers forming zig-zag series for two-thirds of length followed by a dozen transverse rows of 4-minute suckers to tip of arm	Proximal half: 4 rows of minute suckers, the 2 dorsal rows widely separated, the 2 ventral rows closely set in a zig-zag pattern
Rostrum	Soft	Hard					
Dorsal protective membrane	Normal width	Little developed	Very broad, almost completely covering suckers				
Tentacular club	5-6 longitudinal rows of suckers, median row moderately enlarged		Slender 8 longitudinal rows of suckers slightly enlarged in third row	8 longitudinal rows, central 3 suckers greatly enlarged. Dorsal row with few enlarged suckers	8 rows of small subequal suckers	5 longitudinal rows of suckers, median row with 3 greatly and 2 moderately enlarged suckers	Narrow, with 10-14 rows of minute, equally sized suckers
Swimming membrane	Not extending proximally beyond base of club		Not extending beyond base of club			Extending proximally beyond base of club	
Cuttlebone	Not acuminate at ends, sides parallel. Weak spines visible in juveniles, but in adults embedded in chiton. Striated zone not extending beyond midpoint of length	Acuminate at both ends. Spine also visible in adults. Striations sometimes exceeding past midpoint of length	Elongate, oval, dorsal surface with median ridge and fine tubercles. Ventral striations convex, extending 70-80% of bone length with a small posteriorly directed indentation. Spine strong, keel absent	Long, narrow, oval, both ends acuminate. Wings of outer cone united behind inner cone by a rugose, calcareous ledge. Spine very small or absent a short rugose keel present. Striations regularly convex, extending for more than half, but less than three-fourths of length		Width = 1/3 of length. Dorsal surface rose or orange with a faint median groove, ventral surface with striations shaped on a compound curve. Outer cone with two distinct wings, spine strong, prominent and directed dorsally, ventral keel present	Broad, wing-like outer cone, spine absent
Other characters			Series of elongate turbercles at base of fins		Dorsal surface of mantle, head and arms covered with ridge-like tubercles		Round gland and pore visible between fins at posterior end of mantle

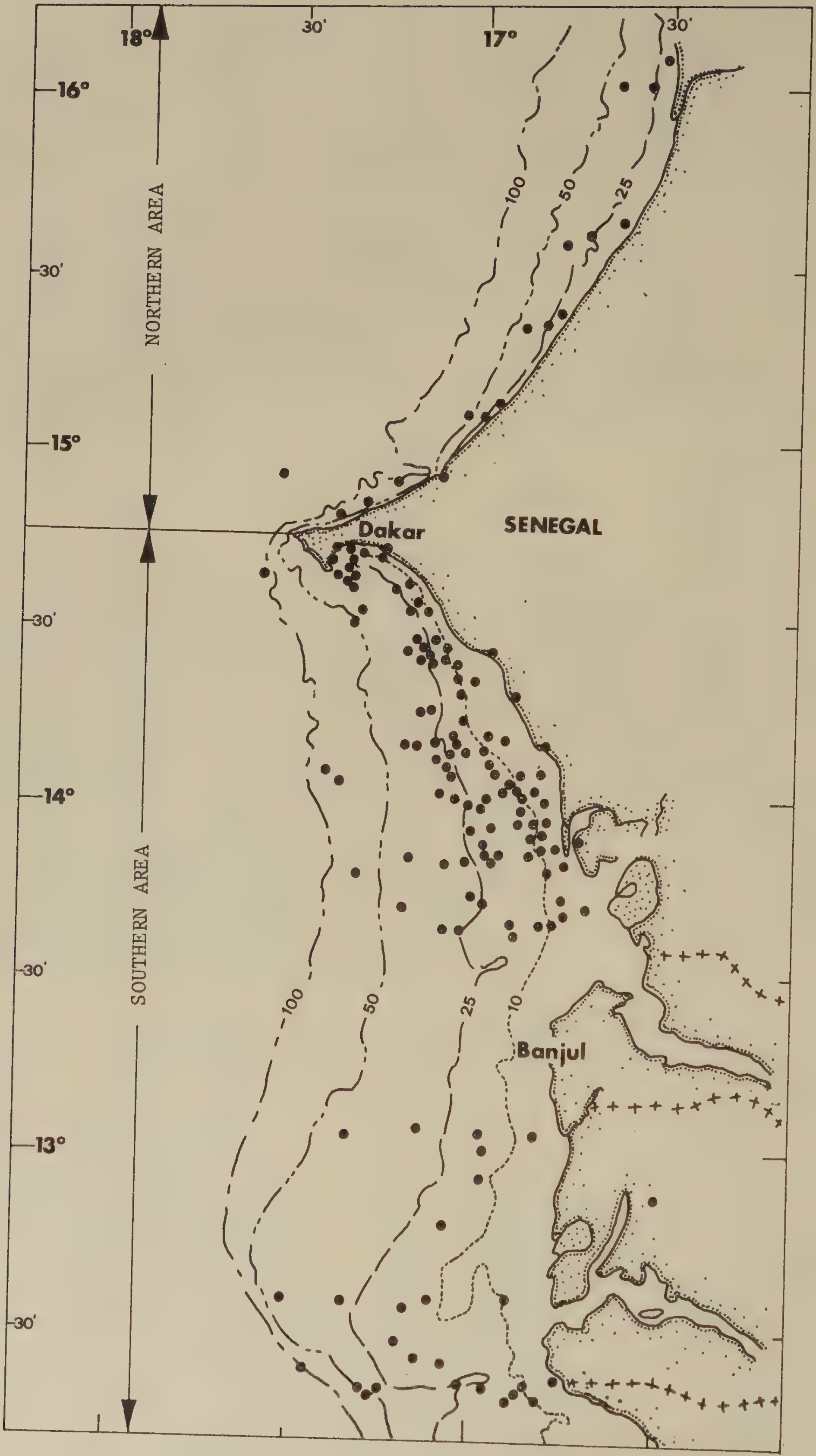

18°
30'
17°
30'
16°
30'
15°
30'
14°
30'
13°
30'
NORTHERN AREA
SOUTHERN AREA
100
50
25
10
Dakar
SENEGAL
Banjul

Figure 1 Locations of trawling by R/V LAURENT AMARO

2.1.2 Commercial pair trawlers

The catches of the commercial pair trawlers and the artisanal landings at M'Bour, Joal and Thiaroye were also sampled. Pair trawlers cover a larger area of the stock distribution and are specially adapted for the *Sepia* fishery. Two sea trips were made in February 1979 and March 1980, of which the first on a pair of vessels of 40 m long and 1 000-hp engine power, with a trawl headline of 120 m and a stretched mesh in the codend of 55 mm. These boats haul at a speed of 4 kn for 80-90 min. Fishing took place during 5 days off southern Senegal, between M'Bour and Sangomar at a rate of 7 hauls per day. Trawling stations were chosen by the skipper according to commercial requirements, at depths of 28-48 m. The length of the captured cuttlefish was measured from the cephalic end of the dorsal mantle to the hind end of the cuttlebone to the nearest centimetre (Figure 3).

The second trip was organized in March 1980, in collaboration with the commercial firm SENEPESCA. Each of the vessels used was 25 m long and had an engine of 375 hp; the trawl had a headline of 80 m and a mesh size of 55 mm stretched in the codend. Figure 2 shows the stations visited. The cuttlefish caught were weighed together and then measured individually to the nearest centimetre. Samples were taken back to the laboratory.

2.1.3 Sampling of landings

2.1.3.1 Industrial fishery: Between January 1979 and June 1980, cuttlefish were measured once a month at the commercial firm SENEPESCA. They were already sorted by category. Within each category, males and females were measured separately until the frequency distribution was established. The weight of the cuttlefish measured was obtained by counting the number of trays per category.

As far as possible, a sample was also taken to the laboratory once every week or every fortnight.

Cuttlefish captured by freezer-trawlers could not be measured by us. As these trawlers operate on the same grounds and use the same mesh sizes, we assume that this omission does not bias our sample.

2.1.3.2 Artisanal fishery: During 1977 and 1978, weekly visits were made to the artisanal fishing centre of M'Bour where data were collected on hours of departure and return, fishing locations, depths, gear used and number of fishermen per canoe. A limited number of cuttlefish were measured without distinguishing sexes, and a sample was taken to the laboratory. In 1979 and 1980, this survey was discontinued, but measurements of commercial landings by sex were made at more landing ports, especially Joal and Thiaroye.

2.1.3.3 Treatment of samples in the laboratory: Samples taken to the laboratory were preserved in the freezer and completely unfrozen before being treated. Measurements, weighing and determination of the sexual maturity were carried out on each specimen. The following detailed measurements were taken: the length of the dorsal mantle or of the cuttlebone to the nearest centimetre below, the maximum width of the cuttlebone to the nearest millimetre below (Figure 4), the length of the hood and the ridge of each jaw of the beak to the nearest millimetre (Figure 5), the width of the open mantle at the head-end, to the nearest centimetre below. The weight of the whole cuttlefish was determined to the nearest 5 g on a Berkel grocer's scale and the nidamental gland plus gonad weight to approximately 0.1 g on a Mettler scale. After drying, jaws and cuttlebones were placed in numbered plastic bags.

2.2 Collection of Statistics

In addition to our biological sampling, the catch statistics of a number of trawlers were available. The following data were obtained from 3 pair trawling units: catches per trawl haul by squares of 10 min latitude and longitude for the period June 1976 to June 1979 and the catches by haul and by depth of the unit we used in March 1980 for our exploratory campaign. The research centre's archives contained catches per net set per commercial category of a SOPAO freezer-trawler for the period 1973-75.

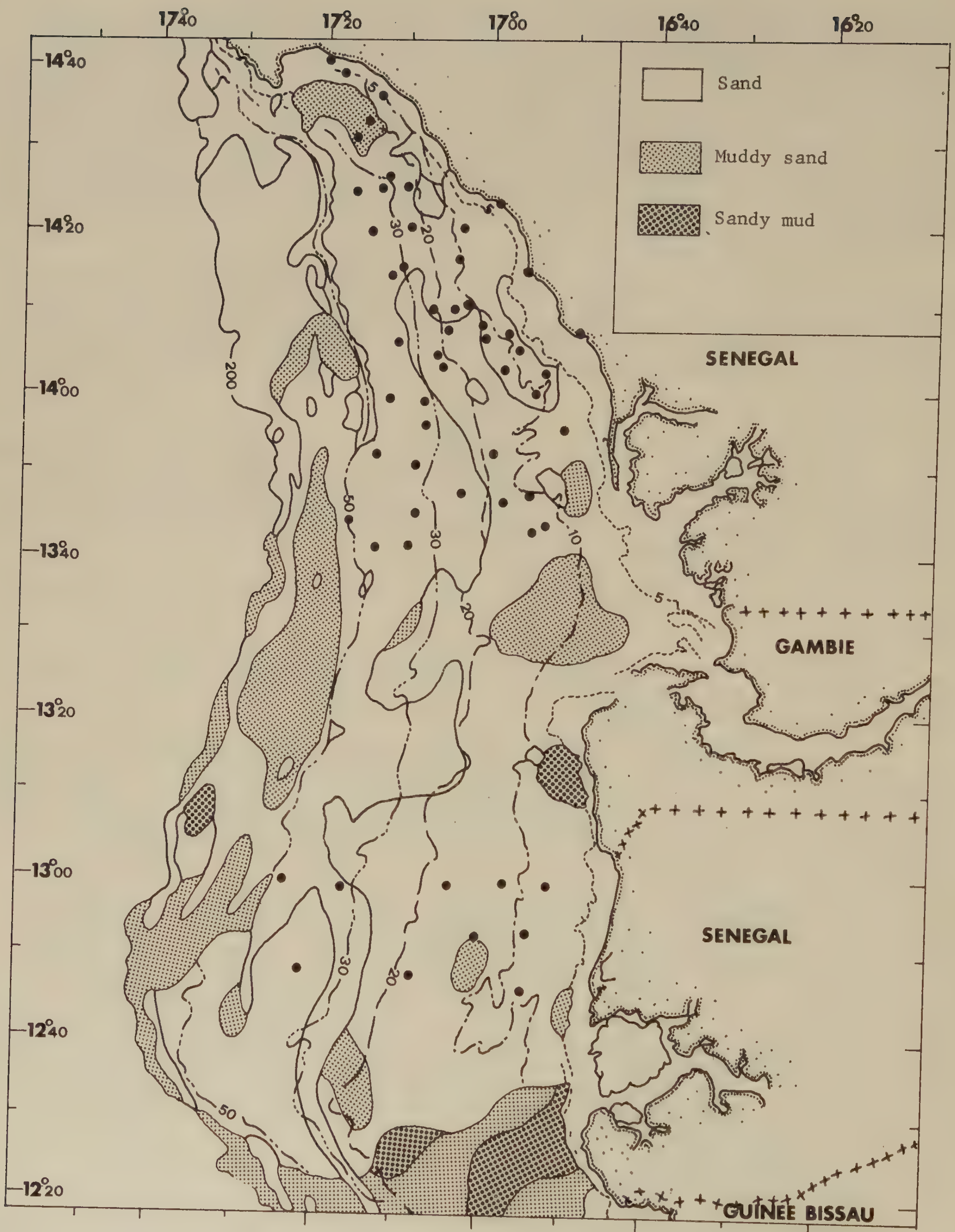

17°40
17°20
17°00
16°40
16°20
14°40
14°20
14°00
13°40
13°20
13°00
12°40
12°20
Sand
Muddy sand
Sandy mud
SENEGAL
GAMBIE
SENEGAL
GUINÉE BISSAU
200
50
30
20
10
5

Figure 2 (●) Experimental trawling stations of pair trawlers in March 1980

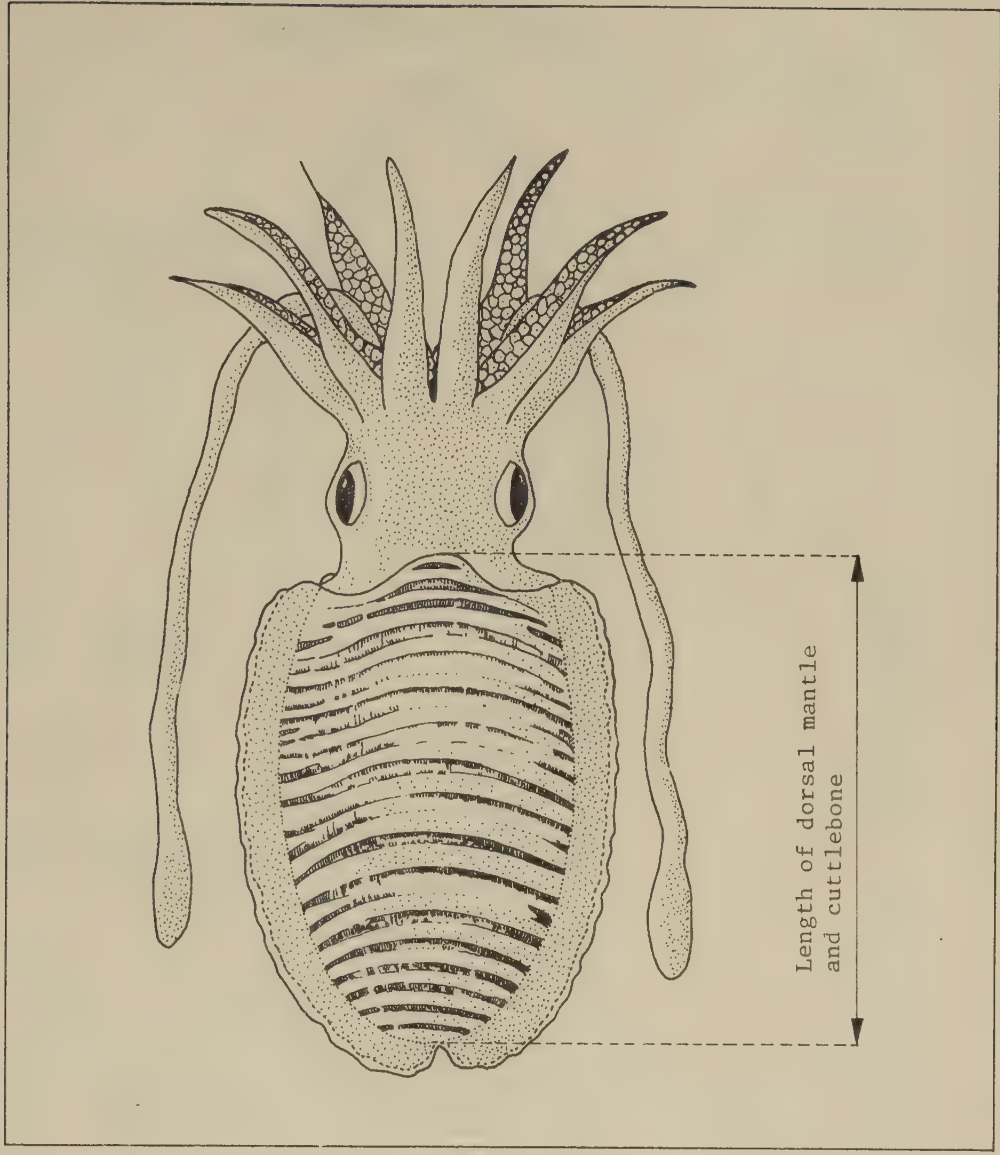


Figure 3 Measurement of *Sepia officinalis hierredda* dorsal mantle

3. DISTRIBUTION

3.1 Seasonal Variations in Abundance and Size

3.1.1 Introduction

Like most other cephalopods, cuttlefish perform seasonal migrations. Seasonal geographical and bathymetrical distribution patterns vary with size. This study therefore places a great emphasis on seasonal variations for which fishery statistical data were used. Unfortunately, no data on the fishery in the Gambia was available.

3.1.2 Geographical variations in abundance and size distribution

3.1.2.1 Abundance: *Sepia officinalis hierredda* was reported on the coast of Africa from 20°N to 10°S by Adam (1941, 1952 and 1960), Garcia Cabrera (1968), Morales and Guerra (1975), Allue *et al.* (1977) and Hatanaka (1979). The areas of higher concentrations seem to be located off Cape Blanc, facing Nouakchott, and on the southern coast of Senegal (FAO 1978). Our surveys among fishermen show that other fishing grounds exist in front of Rio Cacheu and on the Guinea coast, north of Conakry (Figure 6).

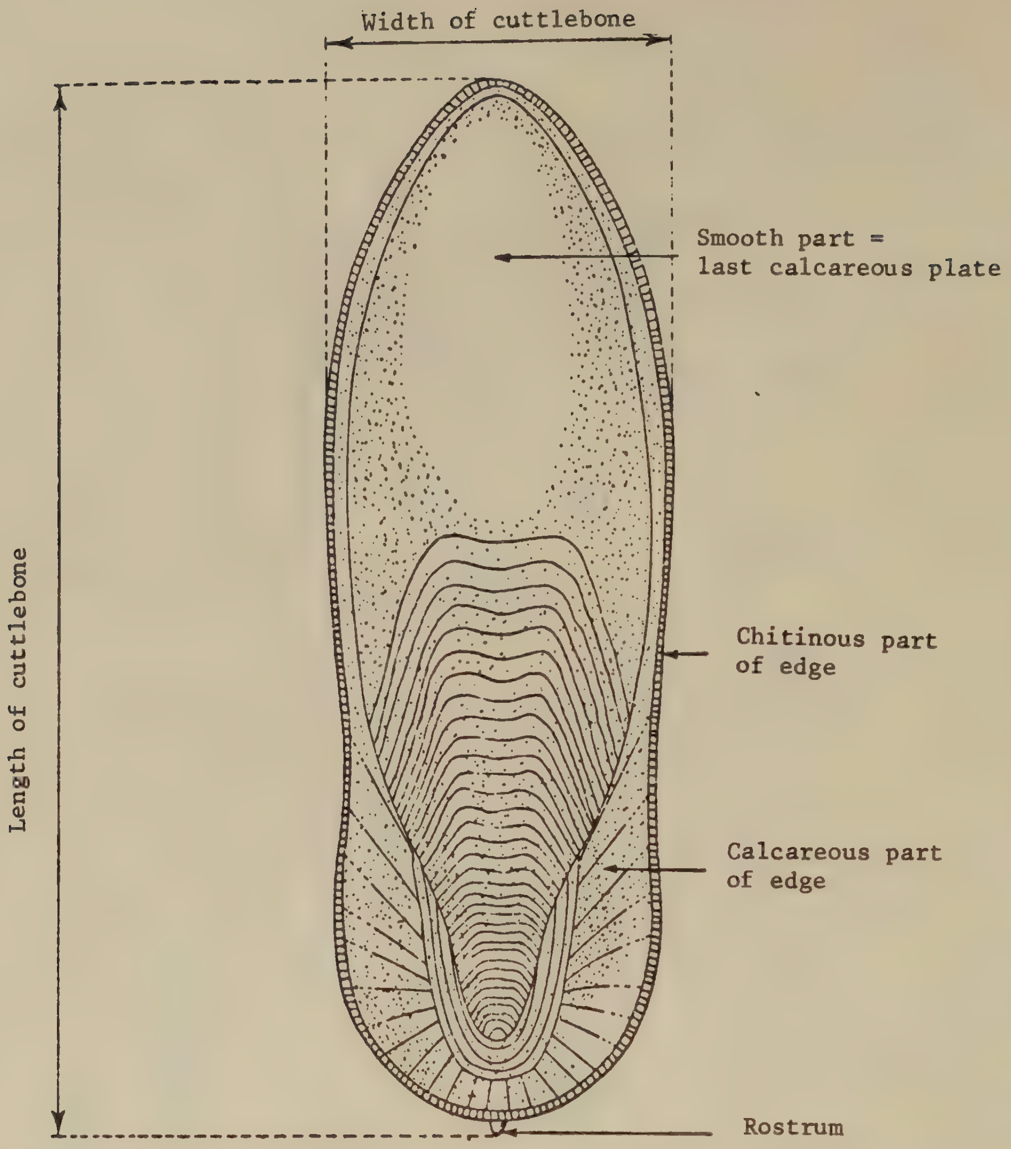


Figure 4 Measurements made on the cuttlebone of *Sepia officinalis hierredda*

Figure 7 shows the spatial variations in cuttlefish abundance on the Senegalese fishing grounds, expressed as the average annual catch per pair trawler net set by 10-min latitude and longitude squares for the period June 1976 to June 1979. Higher yields were obtained off the Petite Côte and Casamance (400 to over 800 kg/set), while the lowest were obtained in the St. Louis sector where a maximum of 50 kg was reached.

An analysis of the average monthly yields in 1976-79 shows variations in abundance per sector: on the Petite Côte the abundance seems to be high between Pointe Sarène and Joal in January, and tends to move south as far as the Gambia between January and June (Figure 8). From July to August, the peak abundance moves back north. In June-July, however, another centre of concentration appears offshore from Pointe Sarène. This seems to move inshore in August. Concentrations are observed in front of Joal and the Saloum estuary in September. They remain there in October offshore from Pointe Sarène. These different concentrations are still present in November and those in front of Pointe Sarène are very close inshore. In December, there is only one area of abundance left which is far offshore.

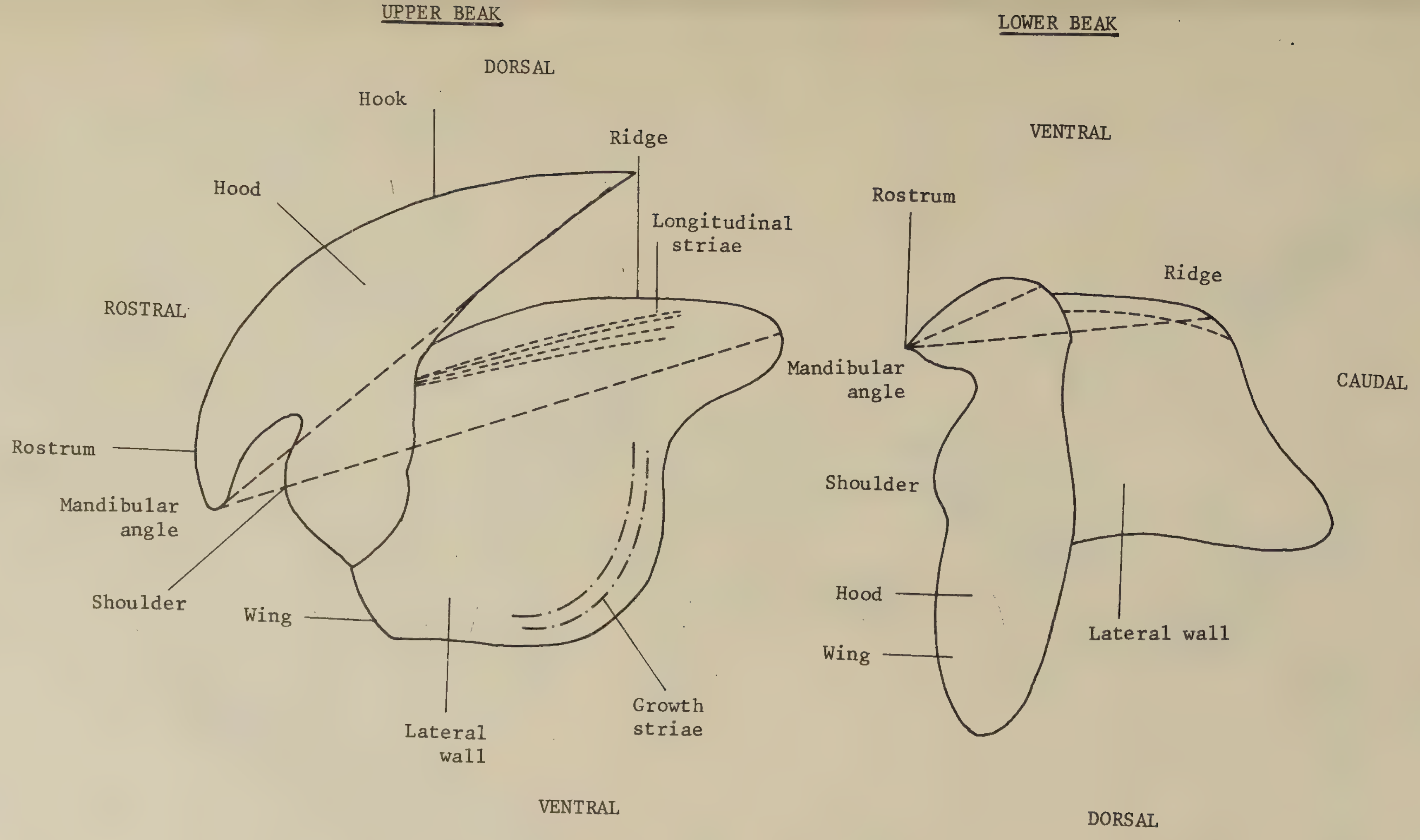

UPPER BEAK
DORSAL
Hook
Hood
Ridge
Longitudinal striae
ROSTRAL
Rostrum
Mandibular angle
Shoulder
Wing
Lateral wall
Growth striae
VENTRAL
LOWER BEAK
VENTRAL
Rostrum
Ridge
Mandibular angle
CAUDAL
Shoulder
Hood
Wing
Lateral wall
DORSAL

Figure 5 Measurements made on beaks of *Sepia officinalis hierredda* (after Mangold, 1966)

a - length of upper beak hood
b - length of upper beak ridge
c - length of lower beak hood
d - length of lower beak ridge

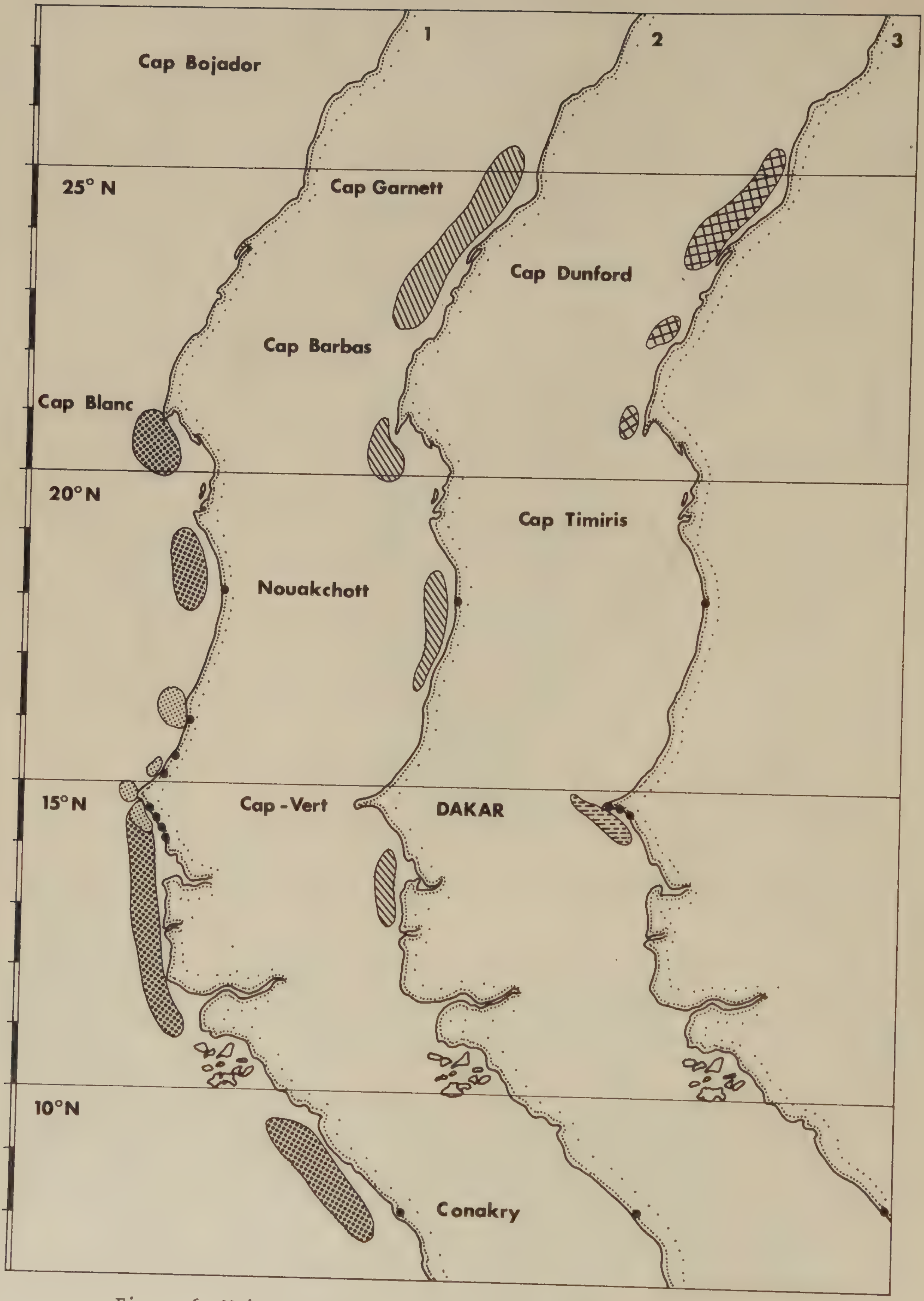

1
2
3
Cap Bojador
25° N
Cap Garnett
Cap Dunford
Cap Barbas
Cap Blanc
20° N
Cap Timiris
Nouakchott
15° N
Cap - Vert
DAKAR
10° N
Conakry

Figure 6 Main cephalopod fishing areas in West Africa

cuttlefish 1 - trawl fishery ▩ artisanal fishery ▩
octopus 2 - trawl fishery ▨
squid 3 - trawl fishery ▩ artisanal fishery ▩

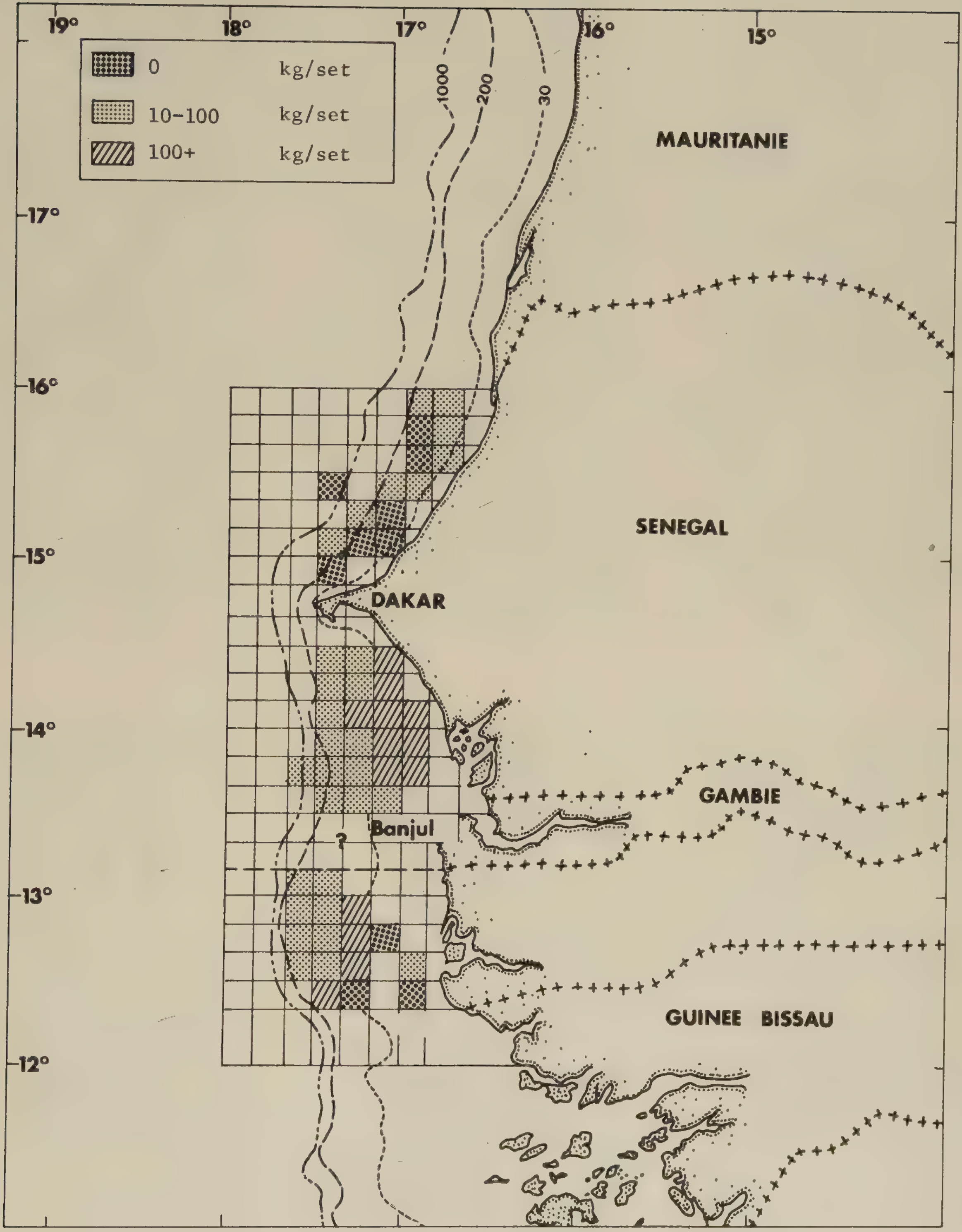
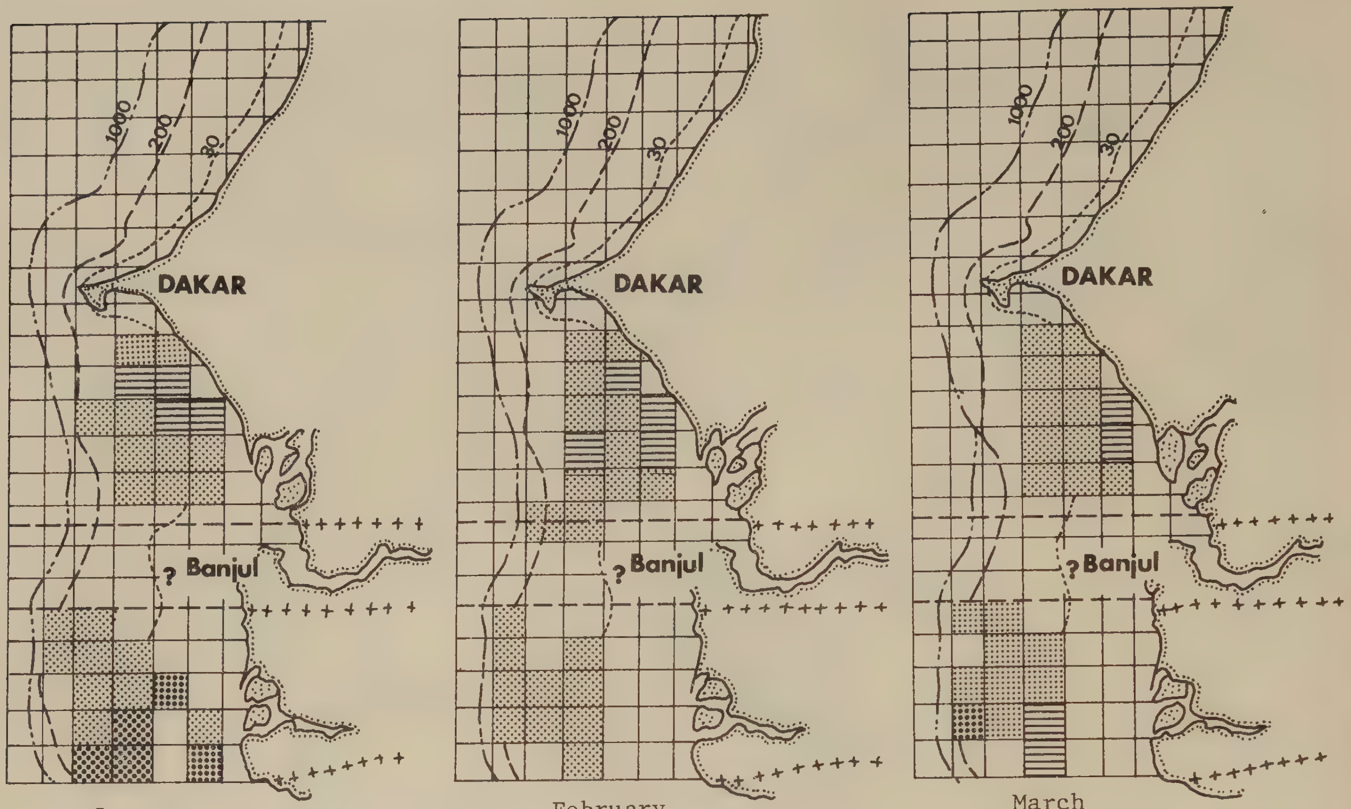

19°
18°
17°
16°
15°
0 kg/set
10-100 kg/set
100+ kg/set
1000
200
30
MAURITANIE
17°
16°
SENEGAL
15°
DAKAR
14°
GAMBIE
Banjul
?
13°
GUINEE BISSAU
12°

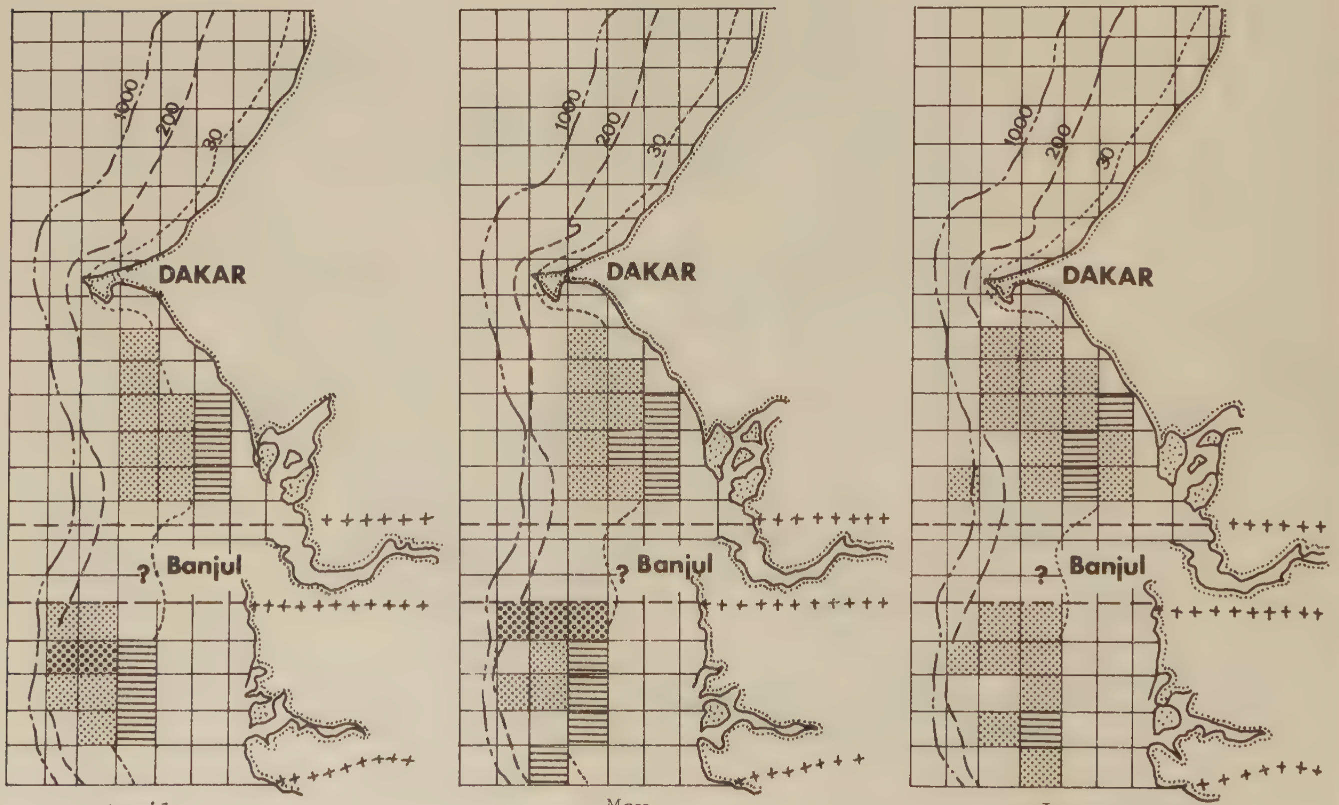
Figure 7 Average annual distribution of pair trawler cuttlefish yields on the Senegalese coasts (June 1976 to June 1979)


1000
200
30
DAKAR
? Banjul

January **A**

February **B**

March **C**

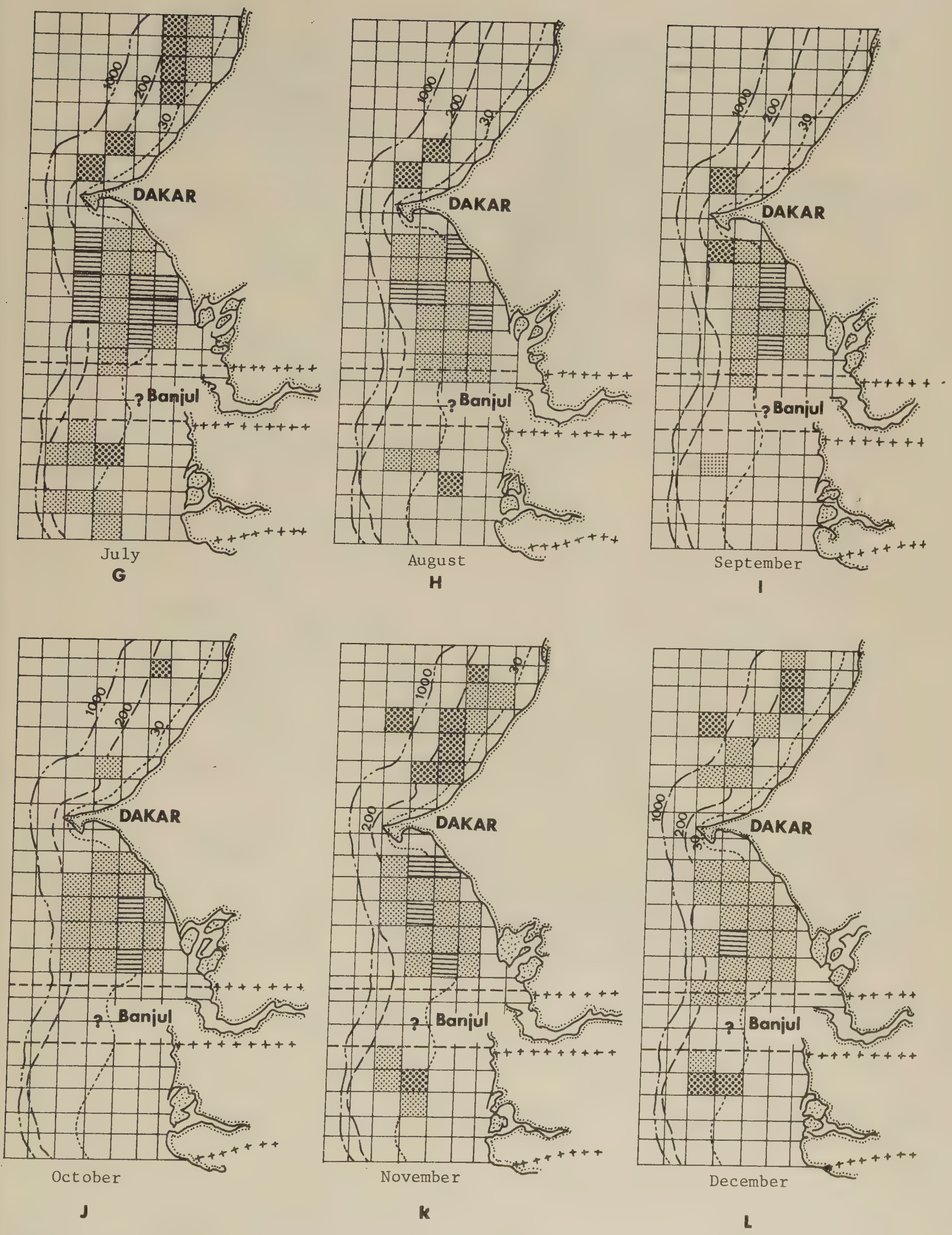

1000
200
30
DAKAR
? Banjul

April **D**

May **E**

June **F**

Figure 8a Time/space variations of monthly average catches of pair-trawlers per haul on the Senegalese coasts (June 1976 - June 1979) - 1st and 2nd quarters


1000
200
30
DAKAR
? Banjul

July
G

August
H

September
I

October
J

November
k

December
L

Figure 8b Time/space variations of monthly average catches of pair-trawlers per haul on the Senegalese coasts (June 1976 – June 1979) – 3rd and 4th quarters

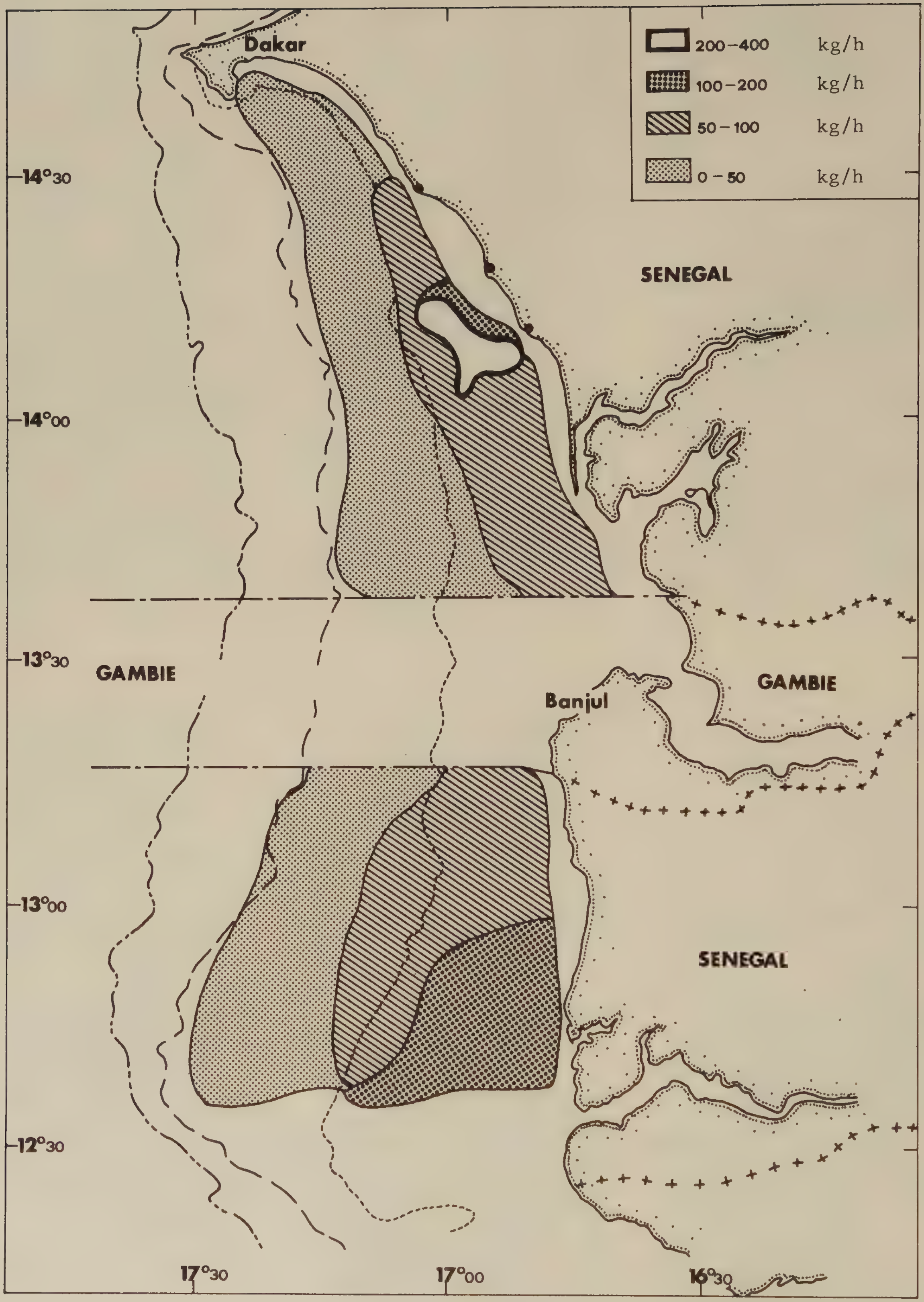

200–400 kg/h
100–200 kg/h
50–100 kg/h
0–50 kg/h
Dakar
SENEGAL
GAMBIE
Banjul
GAMBIE
SENEGAL
14°30
14°00
13°30
13°00
12°30
17°30
17°00
16°30

Figure 9 Distribution of cuttlefish abundance on the Petite Côte south of Dakar (pair trawler data of exploration fishery in March 1980)

The distribution of yields resulting from our March 1980 trawling survey (Figure 9) shows, as was visible in Figure 8, that in this period cuttlefish were most abundant in front of Joal and Sangomar.

In the canoe fishery at Bel Air, M'Bour and Joal, maximum yields were registered in December, March-April and May-June, respectively (Figure 10).

In Casamance, cuttlefish are abundant only between March and June/July (Figure 8). Concentrations first appear at the Guinea frontier and seem to move north. They are found in front of the river in May before starting to descend toward the south in June. Figure 9 also shows that concentrations are highest in March around the estuary.

In the St. Louis sector, where cuttlefish are apparently least abundant (Figure 8), trawling surveys were only conducted in the second semester and yields were low; their variations show a movement of small concentrations from the St. Louis and Mboro grounds to Kayar between July and December. An examination of the log-book of a specialized cuttlefish freezer-trawler over a period of three years (1973-75) shows that north of Dakar these molluscs are low in abundance during the first six months of the year.

To summarize, it appears that cuttlefish are most abundant on the Petite Côte where they are fished throughout the year. They are also abundant off the Casamance, but only from March to June/July. On the northern coast they are least abundant and consequently practically no longer fished.

3.1.2.2 Size distribution: The price of cuttlefish depends on the size, large specimens being sold at a higher price than small ones. A knowledge of the size distribution in the catch is important for fishery management and also for a rational economic exploitation. The frequency distribution of cuttlefish by size category captured by a freezer-trawler (Figure 11) from 1973 to 1975 shows that large individuals of over 1 kg are only captured off the Petite Côte. Small and medium-sized individuals weighing less than 1 kg are fished in all sectors and these are the only ones found off Casamance. This same size distribution pattern was also observed by Chabanne in April-May 1972 (Figure 12). Large cuttlefish are caught only from October to May. Trawlers start catching them in small quantities offshore from Kayar in October, then at M'Bour in January, and at Joal-Sangomar from February-March. Once, in October 1977 a few specimens were caught on rocky grounds offshore from Pointe Sarène. Artisanal fishermen start to catch them at Yoff and Bel Air at the end of December and the beginning of January, at Ngaparou in January and at M'Bour at the end of January and the beginning of February.

To sum up, the small and medium-sized cuttlefish occur on all Senegalese coastal fishing grounds. Large individuals are only fished on the Petite Côte and only from October to May. They first appear at the Cape Vert peninsula and then increasingly further south as witnessed by local fishermen. They are not caught on grounds further south than Casamance or in Guinea. This northern distribution of large cuttlefish was observed by Bas, Morales and Feliu (1971) on the coasts of the western Sahara for the same species *Sepia officinalis hierredda*. Our study on sex ratios per size class and geographical sector tends to show that on the Senegalese coasts the size distribution is not related to sex.

3.1.2.3 Discussion and conclusion: This study of the geographical variations in abundance and the first data on size distribution lead us to think that two waves of cuttlefish succeed one another on the Petite Côte according to the following scheme: a first wave consisting of cuttlefish of all sizes descends from north to south along the Petite Côte during the cold season and returns to the north from June to August. A second wave of small and medium-sized cuttlefish appears in July in front of Pointe Sarène and moves inshore in August. The possibility that two waves of cuttlefish exist is confirmed by the two spawning seasons which coincide with the passing of these waves.

3.1.3 Variations in abundance and size distribution with depth

3.1.3.1 Bathymetric variations in abundance: The greatest depths at which *Sepia officinalis hierredda* have been caught on the West African fishing grounds are at 120 m offshore from the western Sahara (Garcia Cabrera 1968), at 170 m off Cape Blanc and at 110 m offshore from Nouakchott (FAO 1978). The maximum depth at which we caught this species in Senegal

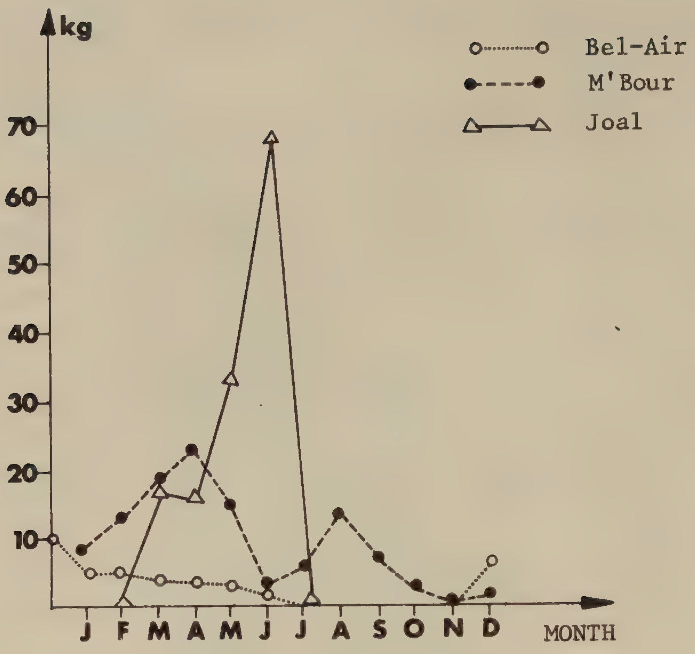


Figure 10 Monthly evolution of cuttlefish yields to pirogues at Bel Air, M'Bour and Joal from December 1978 to December 1979 (kg/pirogue trip)

was 120 m. Further south at 8°N the fishing grounds are at 50 m, but we have no details on the distribution of this species in the area. The variations in abundance need to be studied by depth intervals so that trawlers can develop adequate fishing strategies. We shall try to do this in the present section referring to the Senegalese coasts.

The average monthly catch per haul and 5-m depth interval of a pair trawler over a period of 43 months from June 1976 to February 1980 (Figure 13) shows that cuttlefish are abundant on the fishing grounds at depths of less than 16 m in February-May. After that they move progressively deeper: 16-20 m in June-July, 21-25 m in August, 26-35 m in October, 31-40 m in November and December. From December they again concentrate on shallow grounds and in January they are mostly found at 16-20 m.

Cuttlefish are thus more abundant inshore during the first and offshore in the second semester. This can also be observed in Figure 8. This distribution pattern is confirmed by the variations of the average monthly freezer-trawler catch per fishing hour on grounds shallower and deeper than 25 m in 1974 (Figure 14). Moreover, the catch variations per fishing hour and 5-m depth interval of the pair trawler on which we conducted a cuttlefish trawling campaign in March 1980 (Figure 15) are similar to those observed in Figure 13.

These bathymetric variations of cuttlefish abundance were studied on the fishing grounds of the Petite Côte and Casamance at depths below 50 m. They are also confirmed by the activity of the artisanal fishermen, who operate inshore because of the limited autonomy of canoes. Figure 14 shows that their cuttlefish catches are high from January to June.

The bathymetric movement of the concentrations is also supported by the fact that canoe peak harvest times always occur a little later than those of trawlers (Figure 16). Garcia Cabrera (1968) observed this migration pattern according to depth in the western Sahara area. It was also described by Mangold (1963) who noted that *Sepia officinalis officinalis* moves from the inshore waters to a depth of 120 m in the Mediterranean.

In Senegal, high yields were obtained by pair trawlers on 90-100 m deep grounds during the first years of their activity. However, because of trawl losses (due to the presence of rocks), those ships no longer exploit these grounds.

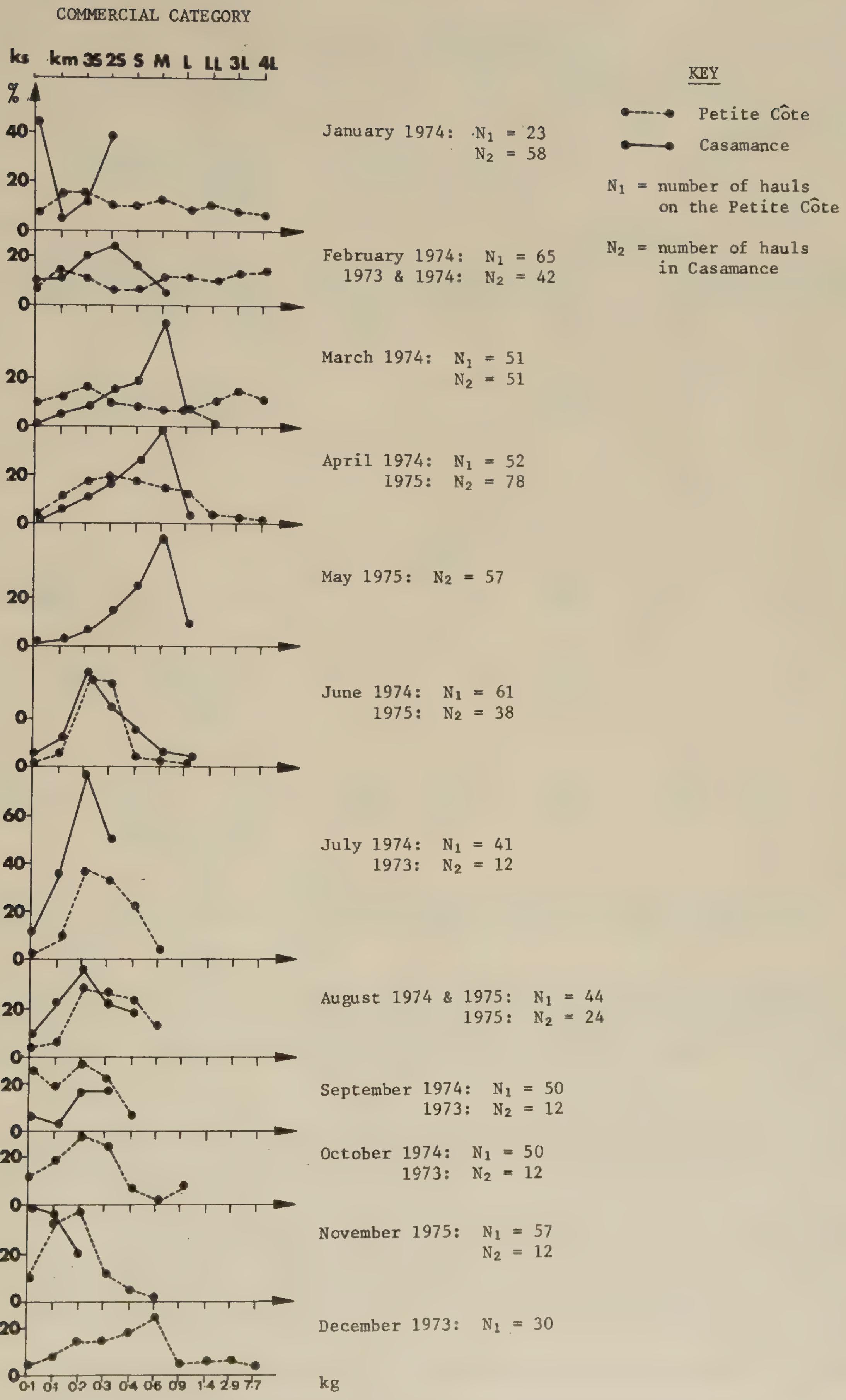


Figure 11 Monthly frequency of commercial categories in the Petite Côte and Casamance sectors (SOPAO freezer data 1973-75)

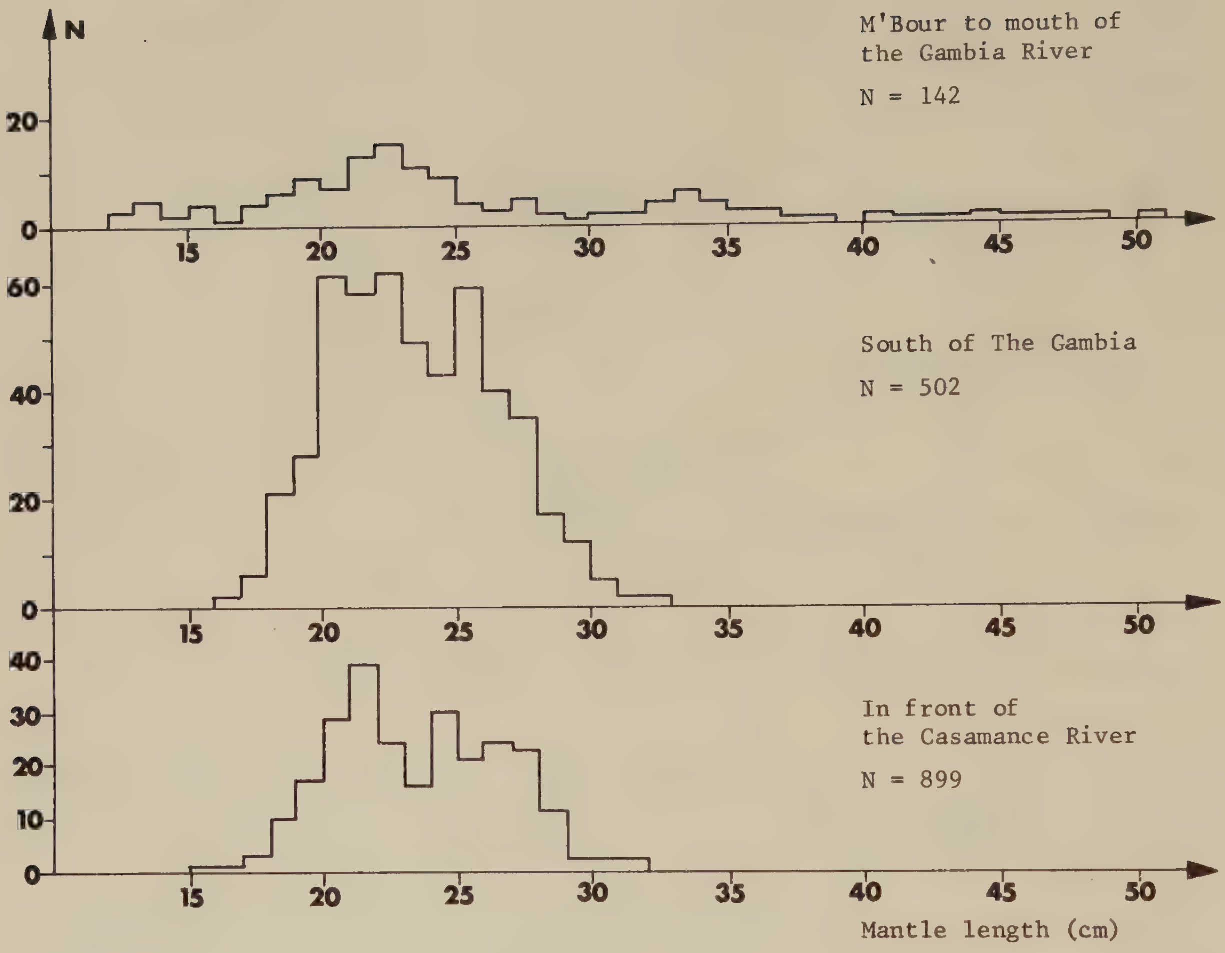


Figure 12 Length composition of catches of an Italian cuttlefish fishing trawler from April to May 1972 on the Senegal-Gambia south coast

3.1.3.2 Bathymetric variations in cuttlefish size: Figure 17 shows that in February large cuttlefish stay on shallow grounds while medium sized and small individuals occupy middle-level and deep grounds of the fishing area reaching depths of 45-50 m on the south coast. In March (Figure 18) large cuttlefish become progressively less abundant from inshore to offshore grounds.

In September-October, large cuttlefish (categories 4L and 3L) are sporadically captured on 90-100 m grounds. In that period the catches contain only small and medium-sized cuttlefish and are made only by trawlers that usually operate on 30-45 m grounds.

This indicates that in February the size of cuttlefish decreases from inshore to offshore grounds, while in September-October it increases in the same direction. Here again we find an annual bathymetric size distribution similar to the one observed by Mangold (1963) in the Mediterranean for *Sepia officinalis officinalis*. This author notes that size decreases from inshore to offshore waters in the cold season and increase from inshore to offshore waters in the warm season.

3.2 Factors Determining Cephalopod Distribution on the Senegalese Coasts

We shall try to define the ecological requirements of *Sepia officinalis hierredda* on the Senegalese coasts based on the available data on geographical and bathymetrical distribution. We shall consider in particular, variations in abundance which, contrary to data

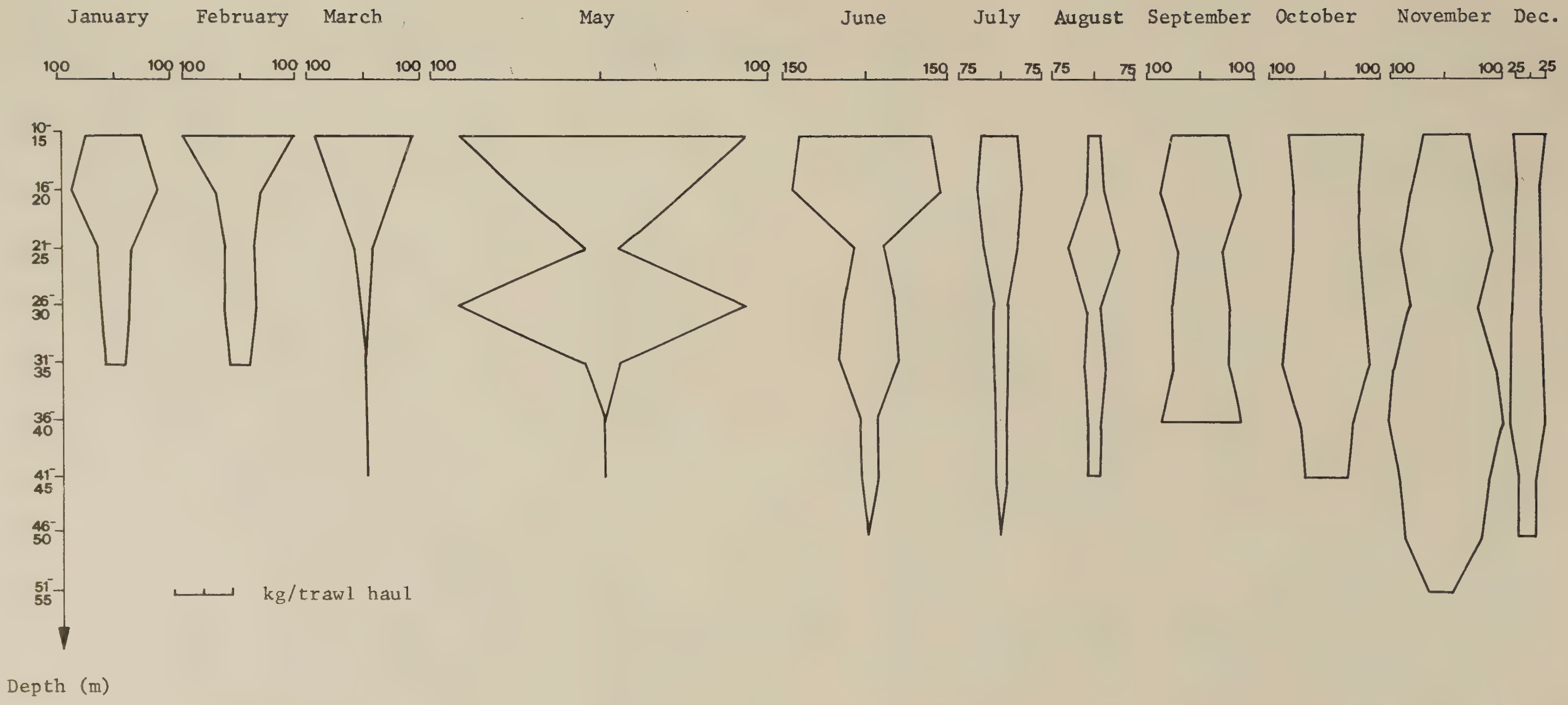


Figure 13 Evolution of a pair-trawler's monthly average yields according to depth from 1976 to 1979

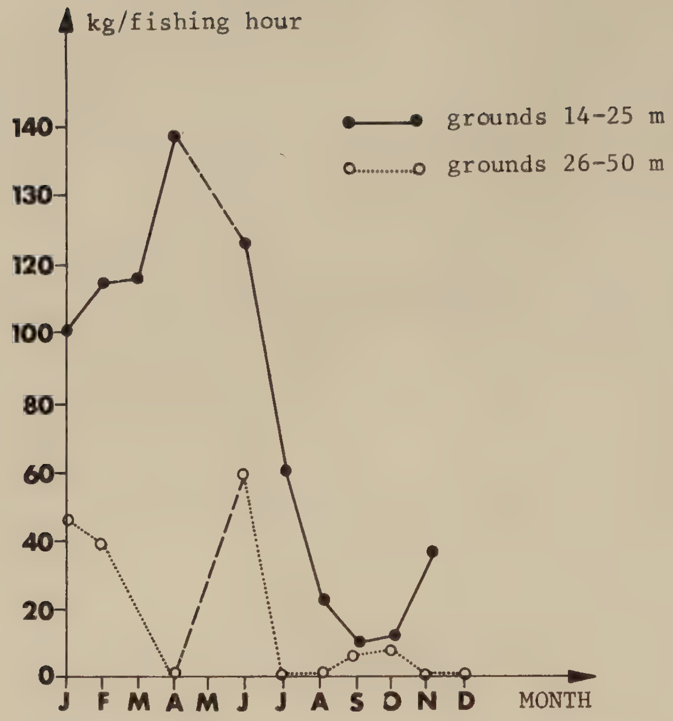


Figure 14 Monthly evolution of freezer-trawler cuttlefish yields in 1974 by depth

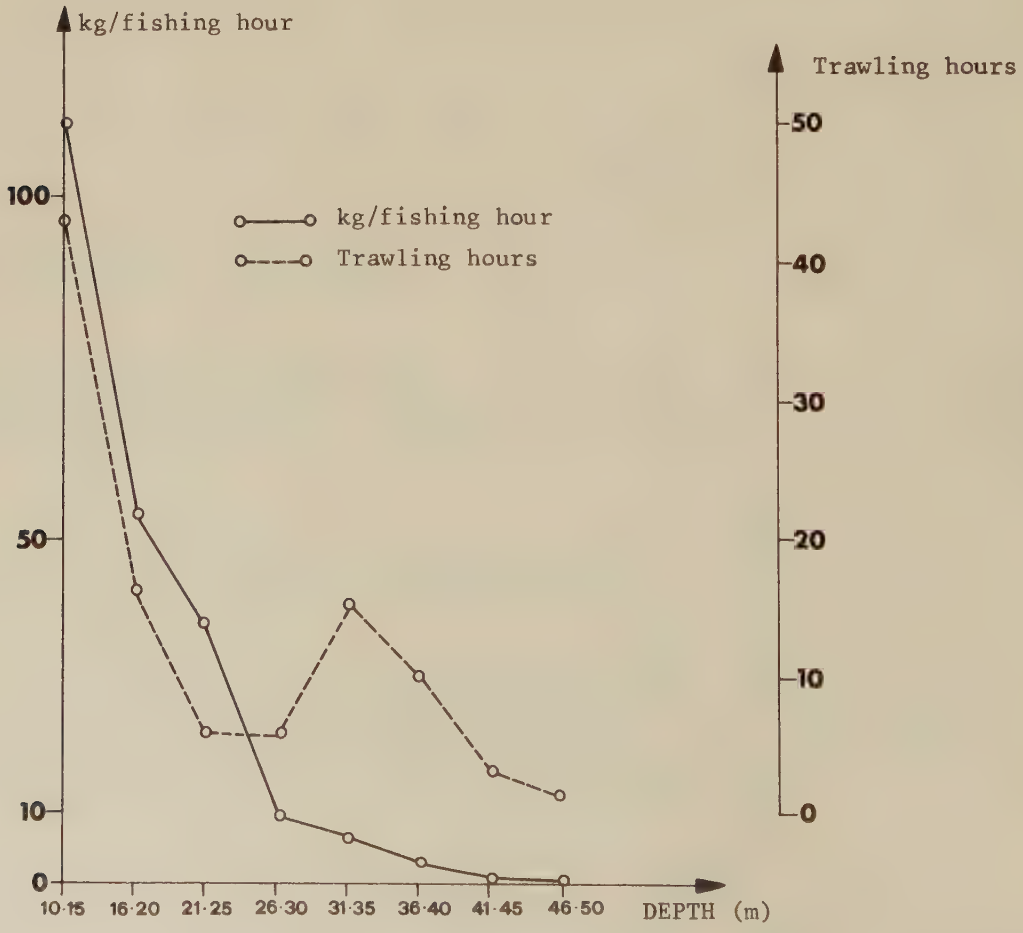


Figure 15 A pair-trawler's cuttlefish yields according to depth on the south coast in March 1980

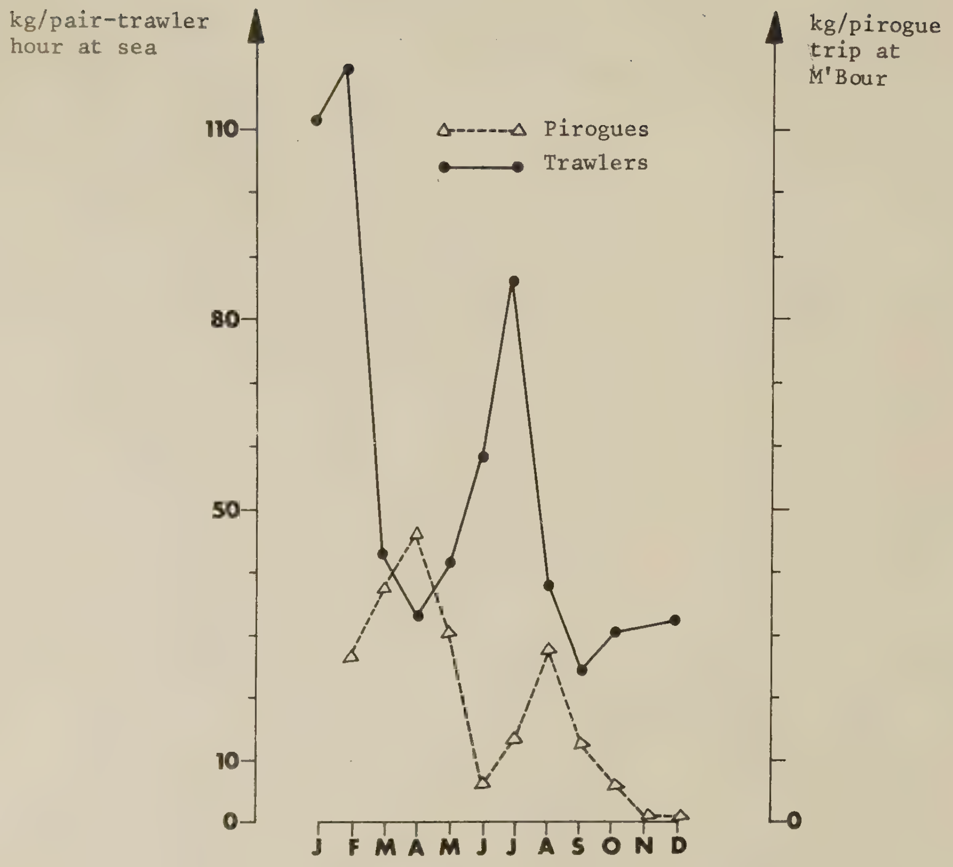


Figure 16 Monthly evolution of average cuttlefish yields of pair-trawlers (1976-79) and pirogues (1979) at M'Bour (the boats fish offshore while the pirogues fish inshore)

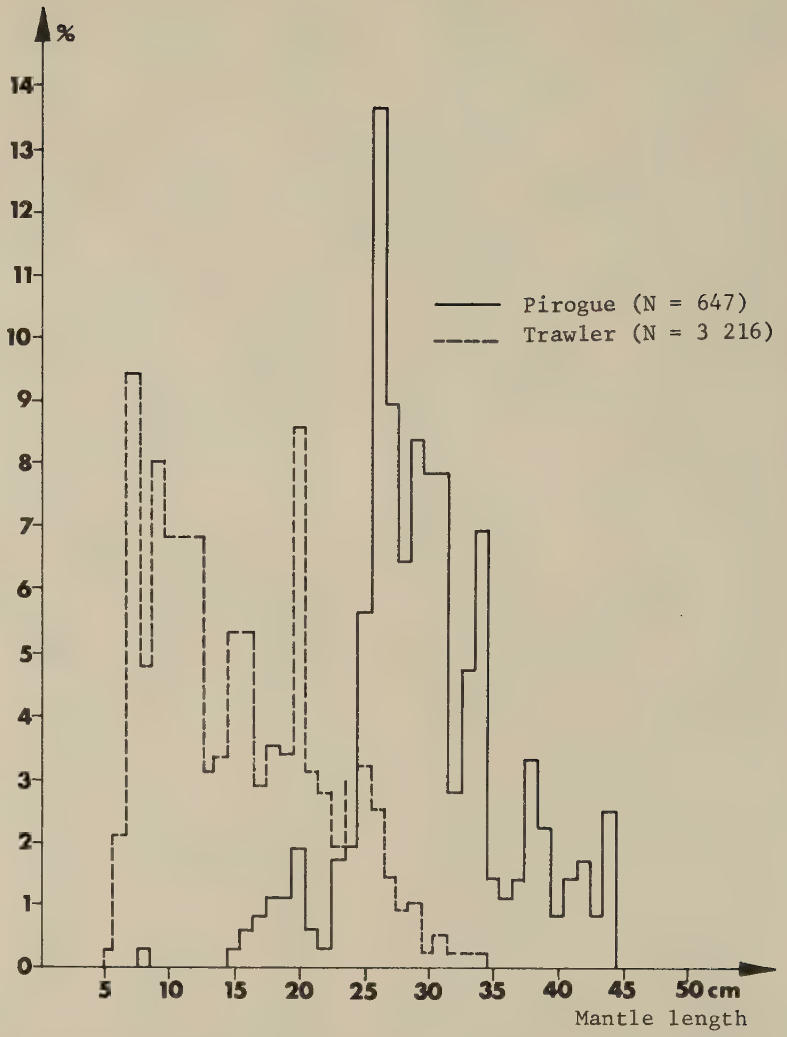


Figure 17 Size frequency distribution of M'Bour pirogue catches and those of a pair-trawler in February 1979 (the pirogues operate inshore and the trawler fishes further offshore)

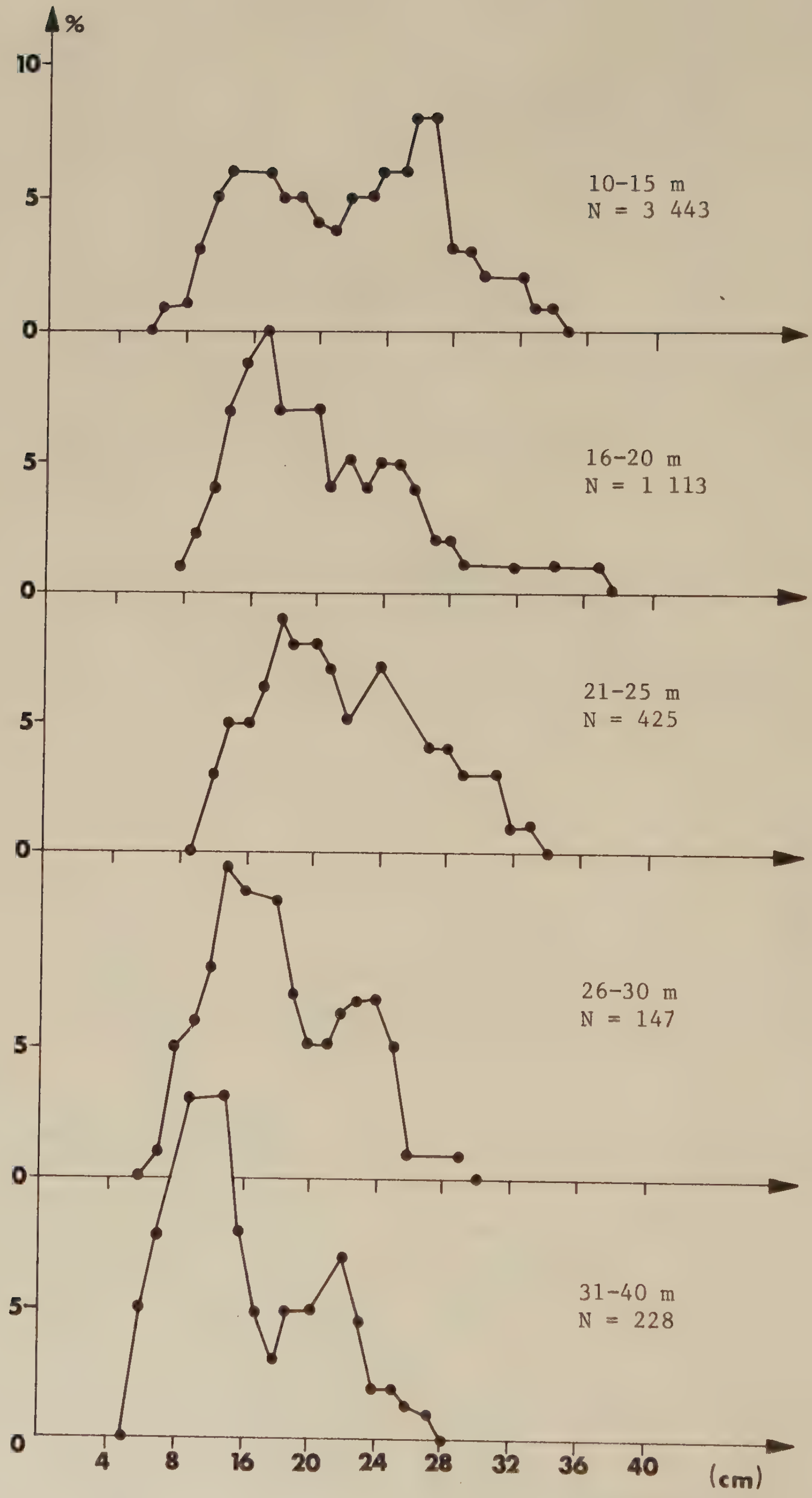


Figure 18 Size frequencies by depth sector on fishing grounds (pair-trawlers), March 1980

on absence or presence of the species, make it possible to determine its preference patterns. This does not mean that we shall attempt to determine the role of each factor as there are close links between the physico-chemical factors and bathymetry. For example, we know that temperature decreases as depth increases. Therefore we cannot define the effect of each factor on distribution. However, on the basis of monthly variations in abundance we shall try to obtain a general idea of this species' behaviour vis-à-vis topography, nature of the fishing ground, extent of its spawning supports and temperature.

3.2.1 Topography

Cuttlefish are caught mainly on the Petite Côte and in Casamance. These grounds have a gradual slope. We have observed that all cuttlefish fishing grounds of the West African coasts are flat. Consequently, at first glance, the topography of the shelf seems to influence the distribution of these molluscs.

3.2.2 Type of fishing ground

Monthly catch averages per pair trawl haul and by type of fishing ground have been calculated from our knowledge of the type of grounds per first square on fishery maps (Figure 19). It seems that cuttlefish are more abundant on sandy and muddy-sandy grounds than on rock. They are not fished on muddy grounds. This distribution is probably due to the fact that cuttlefish try to bury themselves in sand or muddy sand when they are resting (Fischer 1950). Since trawling is difficult on rocky bottoms it is impossible to draw conclusions from the small catches on such grounds. However, cuttlefish seem to prefer mainly sandy or clayey/muddy sand grounds. Garcia Cabrera (1968) noticed this on the coasts of the western Sahara. Mangold (1963) made the same observation on *Sepia officinalis officinalis* in the Mediterranean. However, the evolution of yields per fishing ground type indicates a higher concentration on rocky grounds from December to February, probably related to spawning behaviour as we shall show later.

3.2.3 Spawning supports

Females attach their spawn on supports. Mangold (1963) reports that in the Mediterranean these supports are solid oblong objects. Garcia Cabrera (1968) observed that in the western Sahara area sponges, red algae and *Zostera* are mainly used for this purpose. We have found that on the Senegalese coasts, red, brown and green algae, phanerogams and various objects like branches constitute spawn supports. Trapnets set by artisanal fishermen on shallow fishing grounds are also widely used. This behaviour pattern explains the cuttlefish concentrations in grassy areas, fields of algae and in front of river mouths during the spawning season. Consequently, the presence of suitable supports for attaching spawn is an essential factor for the distribution of cuttlefish in the spawning season.

3.2.4 Temperature

The distribution of most species depends on the hydrological conditions of the marine environment. These conditions can be defined as a group of parameters of which temperature is the easiest to measure and is usually the one for which most data are available. A study of cuttlefish abundance based on this parameter can reveal their possible thermic preference patterns. In order to do this one would need to establish the relationship between cuttlefish abundance and the temperature in a given area. This, however, is impossible because of the lack of data on the temperatures of the fishing grounds. Data are only available for the surface and the 20-m depth zone. In order to simplify, we shall characterize fishing grounds shallower than 20 m by the surface temperatures at M'Bour and the deeper ones by the temperatures of the 20-m grounds. We shall then analyse the variation of the surface temperature in relation to the yields of canoes and trawlers operating inshore from January to May and the variation in temperatures at 20-m depth in relation to the yields of trawlers fishing further offshore from June to December (Figure 20). It appears that from January to June cuttlefish are abundant in waters having a temperature of 17°-23°C, in July-September at higher temperatures of approximately 26°-27°C and from October to December at 20°-24°C. Catches are however higher in the first than in the second semester, in cold rather than warm waters. This is partly due to the spawning behaviour of cuttlefish causing them to concentrate around areas favourable to spawning

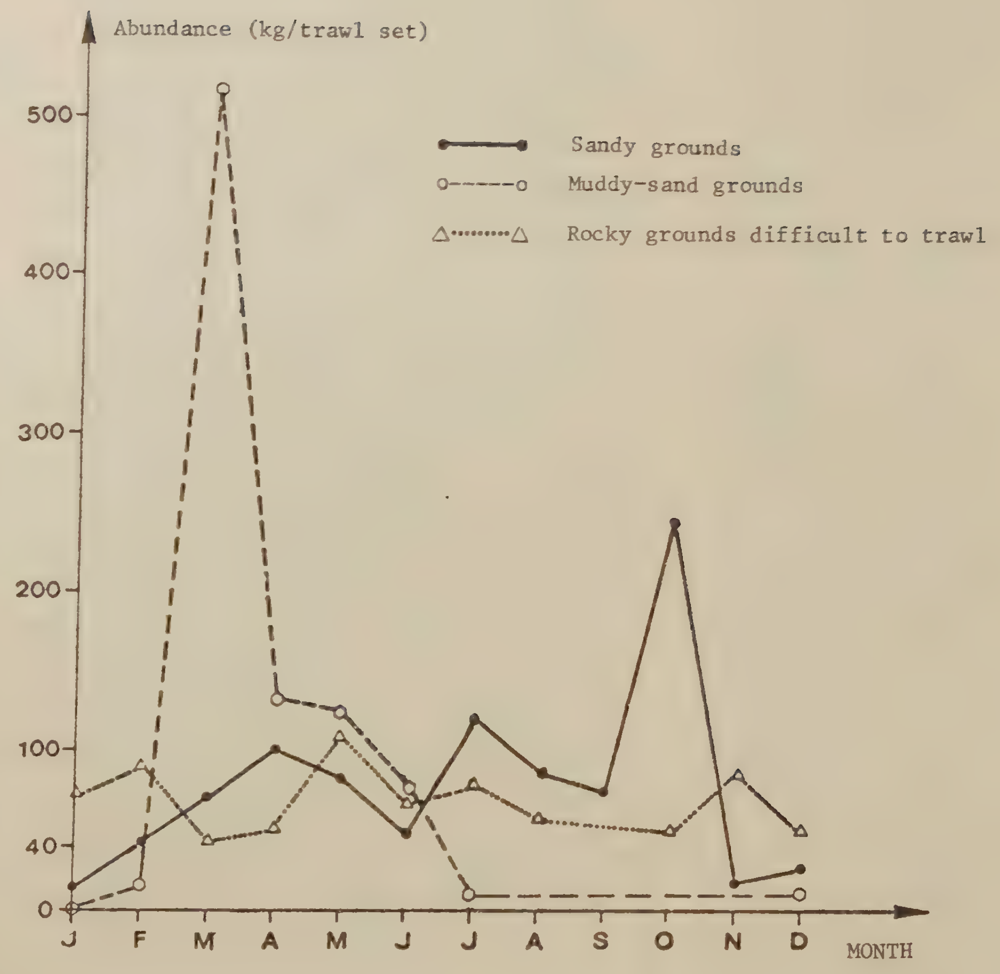


Figure 19 Evolution of cuttlefish abundance by type of fishing grounds

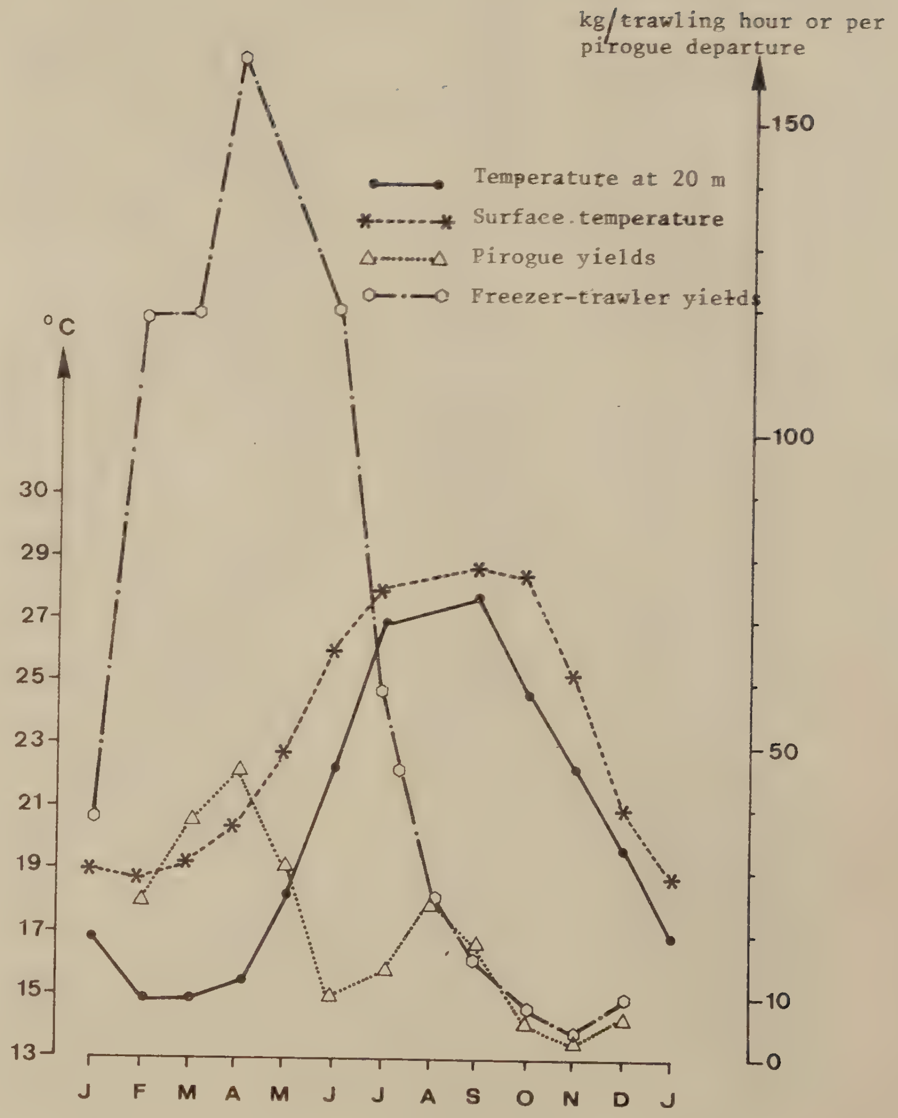


Figure 20 Evolution of yields (of freezer in 1974 and pirogues from M'Bour in 1979) and of surface temperatures (M'Bour) and on 20-m grounds (monthly. temperature average 1974-78)

(for example, presence of supports). Moreover, on deep grounds (90-100 m) inaccessible to fishing, the few positive trawl hauls made in the warm season retrieve many individuals, including some large specimens which are normally only fished inshore during the cold season. The temperatures on these deep grounds are however less than 18ºC below the thermocline (Rebert, pers. comm.). Therefore it seems that cuttlefish prefer waters of 17º-25ºC which means that they return inshore in the cold season (where these temperatures prevail) to find supports on which to deposit their spawn, and that they return to deep water below the thermocline in the warm season. This preference of cuttlefish for cold waters was observed among *Sepia officinalis officinalis* by Mangold (1963). In the Mediterranean this subspecies is abundant inshore in spring time and in the summer at grounds of 60-100 m.

On the West African coasts, the main fishing season is January-May (FAO 1978), when water temperatures of inshore fishing grounds are below 25ºC. Consequently, the thermic preference of *Sepia officinalis hierredda* seems to be between 17º and 25ºC. It should be noted however, that large cuttlefish are more dependent on low temperatures than medium or small-sized ones. In the cold season they are captured inshore in the upwelling waters, and during the warm season they are captured in deep waters below the thermocline. On the other hand, medium-sized and small cuttlfish are caught inshore during all seasons, and those of Casamance seem to withdraw in the very hot Guinean waters from June to July.

In concluding this review of cuttlefish distribution factors we should mention that this aspect would deserve a more detailed study, especially of the hydrological conditions and temperatures of the fishing grounds. Richard (1966) showed the influence of this hydrological factor on the metabolism of *Sepia officinalis officinalis* in the English Channel, where cuttlefish grew more quickly in springtime than in winter. He observed the same phenomenon in aquarium conditions: growth is faster at 20ºC than at 15ºC, and at 15ºC faster than at 10ºC. Lethal temperatures for this species were below 7ºC and above 30ºC (Richard 1966). Other factors may also play a role in determining cuttlefish distribution, as in the case of oxygen which is found in large quantities in upwelling waters and below the thermocline where cuttlefish are abundant. In periods of low salinity and massive deterioration of algae in coastal areas, cuttlefish leave these grounds. It seems however, that salinity does not influence their distribution (Richard 1970).

3.2.5 Tentative interpretation

The nature of the grounds, the presence of supports for depositing spawn and the water temperature seem to constitute the three main factors governing cuttlefish distribution on the Senegalese coasts. Of these, temperature is a major factor since cuttlefish prefer waters of 17º-25ºC.

Besides, they tend to bury themselves in sand and in the spawning season seek supports on which they attach their eggs. To meet these needs, they withdraw on sandy and muddy-sandy grounds at times of sexual maturation. During the spawning season, at any temperature, they assemble in groups in areas rich in algae or grasses with various elongated solid objects which are found on hard sublittoral grounds, sandy grounds inshore and off mostly muddy-sandy river mouths where tree detritus is deposited by rivers. This explains why the south coasts, particularly from M'Bour to Saloum and south of Casamance are areas of high cuttlefish concentration during the spawning season. The north coast in contrast is, because of its steep slope and mostly muddy grounds, unfavourable to the development of larger algae and seagrass. This may account for the absence of cuttlfish on that coast even though its thermal conditions may be suitable.

The search for preferred thermal conditions causes cuttlefish to abandon coastal areas in the warm season for deep grounds further north and below the thermocline. In the next cold season they return to shallow grounds with abundant spawn supports.

It seems therefore that the spawning behaviour is a basic factor in their distribution, linked with temperature variations and character of the grounds.

3.3 Conclusions: Hypotheses on Annual Cuttlefish Distribution on the Senegalese Coasts

The results of our study on cuttlefish distribution lead us to formulate some hypotheses on the annual distribution of *Sepia officinalis hierredda* on the Senegalese coasts (Figure 21). From December to May, cuttlefish migrate from deep water areas to the coast when the inshore waters are cold. The factors determining this migration are unknown, but spawning may play an important role since, as we shall see, the large individuals whose sexual maturation is most advanced arrive first, followed by the medium-sized and small cuttlefish. Presumably, they arrive inshore progressively later from north to south. Some of them die. Occasionally they are gathered by canoe fishermen dead or dying at the surface, where they are spotted because of the seabirds which follow them. Others probably return to deeper grounds.

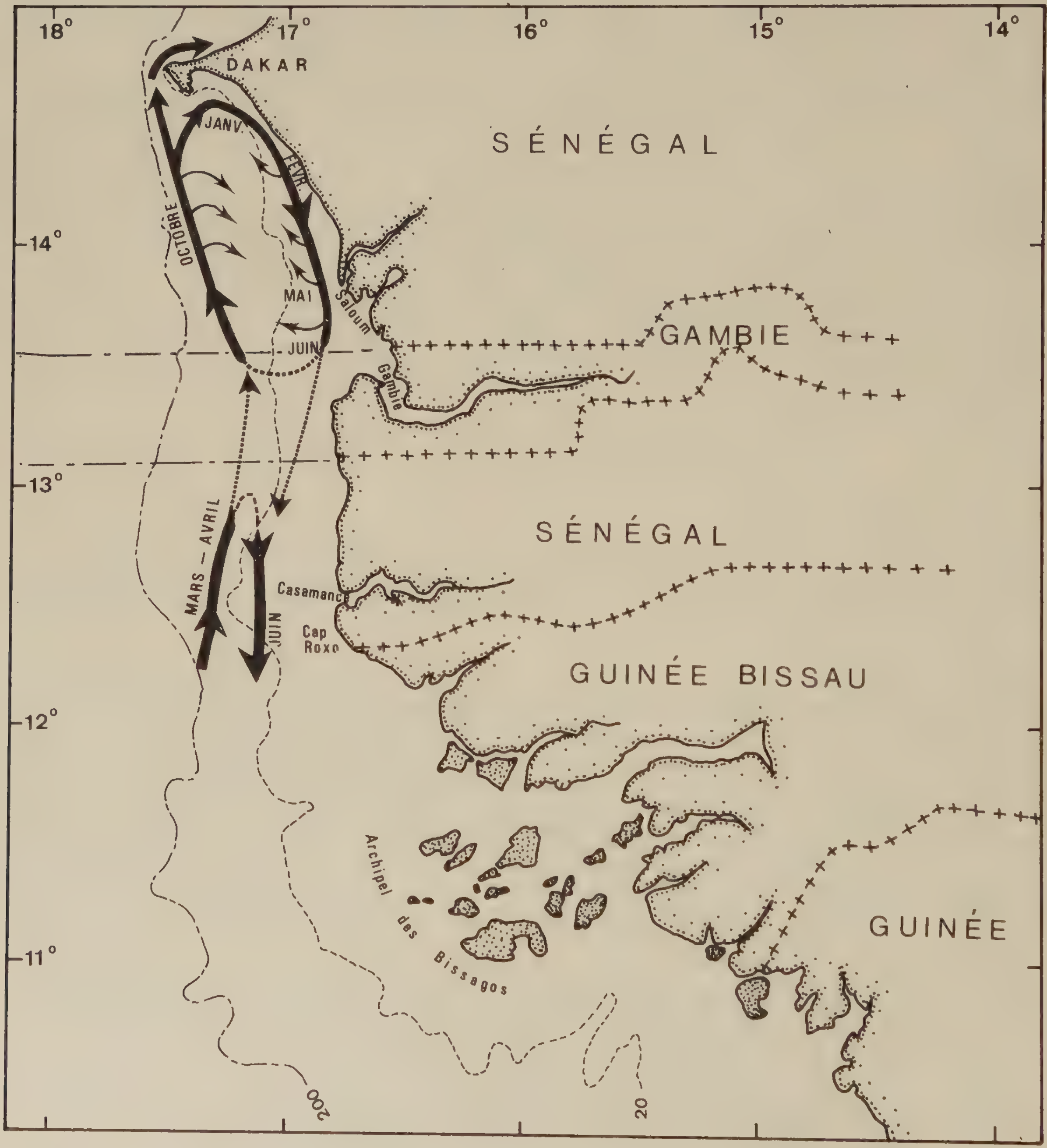

18°
17°
16°
15°
14°
DAKAR
SÉNÉGAL
JANV.
FEVR.
OCTOBRE
14°
MAI
Saloum
JUIN
GAMBIE
Gambie
13°
MARS – AVRIL
JUIN
SÉNÉGAL
Casamance
Cap Roxo
GUINÉE BISSAU
12°
Archipel des Bissagos
GUINÉE
11°
200
20

Figure 21 Pattern of probable cuttlefish migration on the Petite Côte of Senegal

The medium and small-sized cuttlefish that are sexually less mature than the large ones presumably move along the coast toward the south and spawn as they reach maturity. They concentrate mainly in front of Joal and further south from April to June. Some of them go north again staying deeper because of the warm tropical waters that wash the coasts. They are accompanied by young recruits.

Another wave of medium-sized and small cuttlefish make the same journey during the second quarter of the year; in Casamance, most of the cuttlefish probably come from grounds further south, starting in March and returning as far as 13°36'N. Some of them may continue further north while others may return to the south.

This migration pattern is probably the one followed by the majority of the cuttlefish; some of them probably move only from the coast offshore and vice-versa.

A similar scheme was described for *Sepia officinalis officinalis* in the Mediterranean, where Mangold (1963) observed that large cuttlefish move inshore to spawn in February, followed by the medium-sized ones in March-April. Afterwards, they went to deeper grounds of 80-100 m. These are the grounds were immature cuttlefish are captured in spring. They approach the coast to stay in coastal waters in the summer, and return to deep grounds at the beginning of the winter. The following spring, the return of the adults will precede that of the juveniles.

Our study of cuttlefish distribution is far from exhaustive. During the warm season yields are very low on the customary fishing grounds. Large individuals leave these grounds. It would be necessary to know whether *Sepia officinalis hierredda* migrate to zones inaccessible to trawling or whether they go back to other fishing grounds located beyond the Senegalese coasts during that period. Do the Casamance cuttlefish and those found further north constitute two different stocks or a single stock having a complex migration pattern? Most probably they form two different stocks as: (i) the migration patterns appear to be different; (ii) the largest cuttlefish on the Petite Côte are larger than the ones observed in Casamance and even in Guinea as far as 8°N, and (iii) the Casamance cuttlefish have firmer meat than those of the Petite Côte. Their taste is also less appreciated. However, the size composition of the Casamance stocks is relatively homogeneous, and this region is not isolated by any physical barrier. Possibly a major migration cycle with minor 'loops' exists like for the sardinella of the northwest African coasts (Boely 1979). In that case, Casamance would be an area where young cuttlefish perform one of these 'loops'. The existence of a group of small and large cuttlefish belonging to a single stock with different behaviour patterns cannot be excluded.

A large-scale tagging programme and an appropriate and extensive exploration would provide some answers to these questions. A knowledge of the reproductive biology and growth would also be helpful, but these two aspects of cuttlefish biology will engage our attention mainly as factors determining the exploitation methods.

4. BIOLOGY OF REPRODUCTION OF *SEPIA OFFICINALIS HIERREDDA* ON THE SENEGALESE COASTS

Our aim in studying the reproduction will be to learn the size of first sexual maturity, the spawning seasons, locations and the fecundity of *Sepia officinalis hierredda*. These data are necessary for a rational management of the stocks, a rational choice of mesh sizes will prevent overfishing before the cuttlefish reach their first maturity. The market value of juveniles is high. Furthermore, a knowledge is required of the sizes that participate most in stock renewal and of the reproductive capacity which is a dynamic factor influencing the choice of exploitation method.

Cuttlefish reproduction has been studied previously by various authors. We mention the work of Mangold (1963, 1966) and Hatanaka (1979) on *Sepia officinalis officinalis* of the Mediterranean and West African coasts, Garcia Cabrera (1968) on *Sepia officinalis hierredda* of the western Sahara and Ikeda *et al.* (1976) on both subspecies as these authors studied the cuttlefish of fishing grounds in West Africa between 16°30' and 25°N.

4.1 Scale of Maturity

The large number of determinations of stages of sexual maturity that we intend to make requires the application of a method based on criteria that can rapidly be defined. Consequently, as a preamble to this study we must define a scale of sexual maturity meeting that requirement.

Scales of sexual maturity have already been described for cuttlefish. Mangold (1963), referring to *Sepia officinalis officinalis* in the Mediterranean, distinguishes five stages based on size and appearance of the eggs:

- very small, smooth eggs (< 2.0 mm)
- small eggs, smooth or reticulated (2.1-4.0 mm)
- reticulated medium-sized eggs (4.1-6.0 mm)
- reticulated large eggs (6.1-8.0 mm)
- smooth large eggs (6.1-8.0 mm)

In the English Channel, Richard (1967) determined the stage of sexual maturity of cuttlefish in his experimental tanks based on a scale of six stages defined according to the colour of the accessory nidamentary glands. Their colouring changes from white to coral as maturity advances: white, creamy white, beige, orange-yellow, coral. Garcia Cabrera (1968) observed five stages for *Sepia officinalis hierredda*:

- the gland begins to swell
- the glands are completely visible
- the glands are at mid-point of maturation
- the glands have almost reached their maximum development
- spawning begins

Results obtained by an *ad hoc* working party on sexual maturation of exploited species of the Gulf of Guinea (ISRA/ORSTOM 1979), indicate that an appropriate maturation scale for tropical areas should take into account both the macroscopic and the microscopic aspect of the gonads. An example of this work described by Fontana (1969) for the sardinella of Congo should enable a comparison of results of different origins. We have followed the same criteria to establish a scale of cuttlefish maturity that will be practical and less subject to errors of evaluation. Individuals of different sizes were selected, their gonads and eggs described, and size frequencies obtained from the eggs measured.

We have described five practical stages of sexual maturity in females of *Sepia officinalis hierredda* which are summarized in Table 2. The size distribution of the eggs is practically the same as the one in Mangold's scale (1963). These stages were adequate for a study of the spawning season, the size at first maturity and the fecundity.

In this study we shall assume that the female reproduction cycle is simultaneous with that of the males and we shall confine ourselves to a study of the females. Furthermore, we shall consider females at stages 2-5 for the study of periods appropriate for reproduction and females at stages 4 and 5, which we consider mature, for the study of spawning seasons.

4.2 Size at First Maturation

The meaning of this term differs according to different authors who may define it as follows: (a) The size of the smallest maturing or mature female observed; this size depends on the number of individuals sampled, the selectivity of the fishing gear and the time of sampling. It does not represent the maturity of the population and has no value from the stand point of population dynamics; (b) The size beyond which all females are maturing or mature, and (c) The size at which 50 percent of the individuals are maturing or mature. The last two definitions are those most widely used in population dynamics. However, the percentage curve of maturing or mature females based on size is generally sigmoid. The size beyond which all females are maturing or mature is therefore not easily estimated. Moreover, the fecundity of the stock calculated on the basis of this definition is probably underestimated. On the other hand, the last definition is more convenient and allows a less biased fecundity calculation. It will be used here.

Table 2

Scale of sexual maturity in *Sepia officinalis* females

Stage	Appearance of gonad	Appearance of eggs	Size of eggs
1 immature	small yellowish-white gonad plated on the upper side of the ink pouch	small yellowish eggs	less than 2 mm
2 maturation	medium-sized yellowish gonad, medium-sized well-separated eggs on all or part of the outside of the gonad	small eggs clearly visible, medium-sized reticulated or uniformly whitish ovoid eggs	less than 2 mm 2-4 mm
3 pre-spawning	large yellow gonad occupies the concave rear part of the cuttlebone, egg clusters increasing in size from the interior to the exterior. Greenish jelly-like mass occupies the rear part of the gonad	small eggs medium-sized eggs large yellow round and reticulated eggs	less than 2 mm 2-4 mm 4-6 mm
4 spawning	appearance same as in stage 3, but with smooth eggs free in the gonad sheath or engaged in the oviduct. Yellow and white areas frequently on the rear part of the gonad	small eggs medium-sized eggs large eggs very large, smooth and transparent eggs	less than 2 mm 2-4 mm 4-6 mm 5-9 mm
5 post-spawning	small yellowish-white gonad in an almost empty flaccid sac	small eggs medium-sized eggs large eggs	less than 2 mm 2-6 mm

Having found mature females throughout the year, we calculated the percentages of females in stages 2 to 5 by size class and by month. Figure 22 estimates this size at 13 cm after fitting of a curve to the cluster of points each of which represents an average of three values. According to this method of calculation, this size corresponds more closely to the average size at first maturation. Garcia Cabrera (1968) finds that the size at first spawning is 14 cm for the western Sahara. These values are higher than the smallest mature size (11 cm) observed by Mangold (1963) in the Mediterranean for female *Sepia officinalis officinalis* and lower than the size of 15 cm at which all female of this subspecies are mature (Mangold 1966). Therefore it seems that 13 cm is the average size at first maturation for the species *Sepia officinalis*, based on samples taken throughout the year.

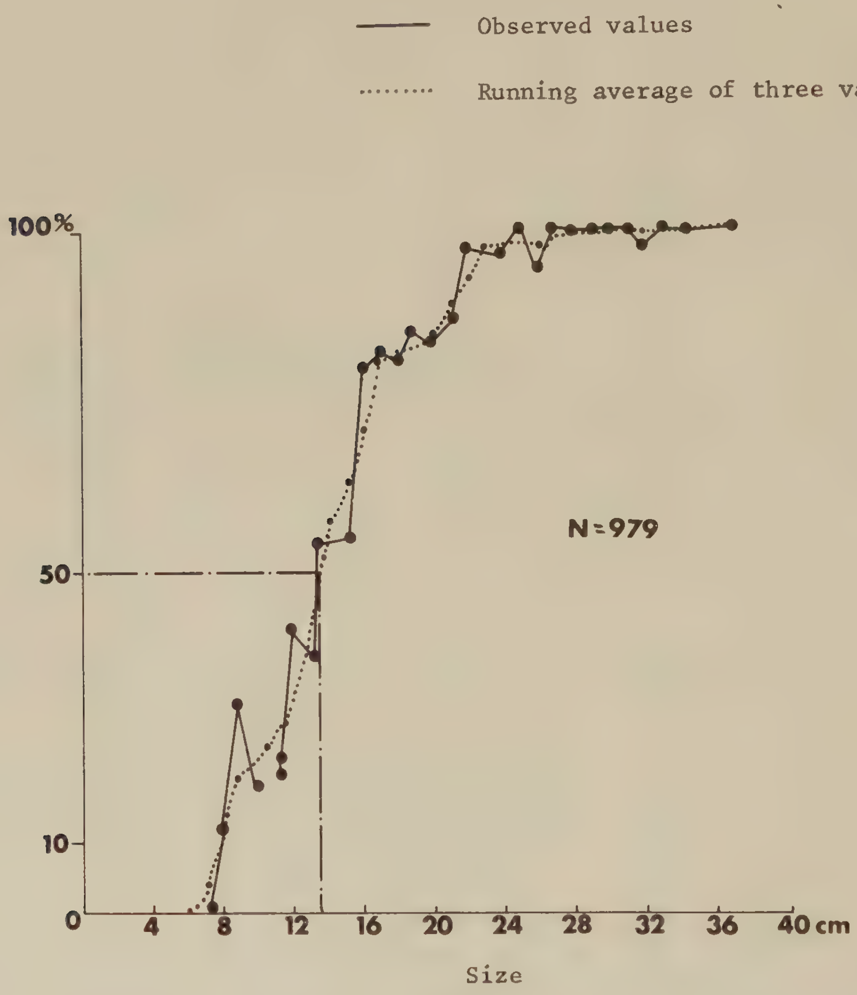


Figure 22 Proportion of maturing females (stage 2 to 5) among females captured according to size

4.3 Indexes of Reproduction

4.3.1 Definitions of indexes

The biological timing of reproduction can be studied from a number of indexes. A critical inventory of these indexes was made by ISRA/ORSTOM (1979) for the fish species exploited in the Gulf of Guinea. Six indexes were mentioned: (a) the percentage of mature females; (b) larval abundance; (c) the gonad-body weight relationship; (d) the liver-body weight relationship; (e) the sex ratio, and (f) the condition factors. It appeared that none of these indexes utilized separately enables us to obtain an accurate image of reproduction and its seasonal variations without risk of error. It will therefore be necessary to use several indexes and compare the results obtained.

There is however, no larval phase in the life cycle of the cuttlefish, and young individuals live on the bottom. The 25-mm mesh trawl (bar) which we use, catches very few of them. A digestive gland which is difficult to isolate and measure replaces the liver.

The complex migration cycle makes a study of the sex ratio difficult and prevents dissociation of the effect of reproduction from that of migrations on total body weight.

For these reasons the use of young cuttlefish abundance, digestive gland weight variations, sex ratio and condition factors are not considered useful indexes. We finally decided to rely only on the percentages of mature females and the gonado-somatic ratio (GSR).

We have also made use of other characteristics of cuttlefish. These molluscs have nidamental glands whose function is to secrete a substance for protection of the egg. Spawning is accompanied by an emission of this substance which envelops the egg which is then attached to a support. The egg cluster attached in this way is shaped like a bunch of black grapes (sea grapes). Large weight variations affect the nidamentary glands during the sexual cycle. Variations in the nidamental-somatic ratio (NSR) could therefore, like those of the GSR, reflect the different stages of sexual maturity. This has led us to adopt two other reproduction indexes, the NSR and spawning intensity.

Four indexes were ultimately used in this study:

(a) The percentage of ripe females of the total number of females samples;

(b) The gonado-somatic ratio (GSR), defined as the relation between gonad weight (W_g) and total body weight (W_b) or soma weight ($W_b - W_g$). It is expressed by two different formulae, depending on the author:

$$GSR_1 = \frac{W_g \times 100}{W_b} \quad \text{and} \quad GSR_2 = \frac{W_g \times 100}{W_b - W_g}$$

The first formula, although not the accurate definition, produces results that vary in the same way as those of the second. It will be used here as it is easier to calculate.

(c) The nidamental-somatic ratio (NSR) - as in the case of the first GSR formula, the following less accurate definition will be used here for convenience:

$$NSR_1 = \frac{\text{weight of nidamental glands}}{\text{total body weight}} \times 100 = \frac{W_{ng} \times 100}{W_b}$$

the correct definition being $NSR_2 = \dfrac{W_{ng} \times 100}{W_b - W_{ng}}$

(d) Spawning intensity

4.3.2 Critical study of the indexes

All the indexes defined previously and adopted for this study can be used to determine the spawning seasons. This term will be used here to designate sexual maturation from stages 2 to 5, including spawning which corresponds to the emission of eggs and coincides with stages 4 and 5.

High proportions of mature females, and high GSR and NSR indexes suggest either conditions favourable to gonad maturation or a high proportion of large-sized females. Therefore we shall study the evolution of these indexes by size class to eliminate the influence of the latter factor on reproduction. It should be noted that the variations of these indexes reflect the variations of reproduction at the individual level. If the abundance is taken into account they would indicate the variations at the population level. Thus, variations of proportions of ripe females weighted by an abundance index would reflect the evolution of spawning intensity. This is also expressed by variations in spawning abundance. GSR and NSR should however, be regarded with caution. Their variations may be due to the degree of fullness of the stomach or ink sac rather than to variations of gonad or nidamental gland weight. During our dissections we observed, however, that these organs were almost completely empty, justifying us in omitting the bias they could introduce in GSR and NSR indexes. The fecundity estimate based on spawning is also generally biased. In fact, the number of eggs laid by a female could be overestimated since an egg cluster may be the result of the spawning of several females (Tinbergen 1939); a single female can also attach her spawn on several supports. On the other hand, fecundity may be underestimated when the eggs are collected by a trawl. This gear usually breaks up clusters.

Furthermore, large cuttlefish are not captured from May to November. The various indexes adopted should enable us to determine the following:

(a) In small and medium-sized cuttlefish available at all times, the periods favourable to gonad maturation and those of intense spawning activity; and
(b) In case of large cuttlefish, the stage of their sexual maturity during the period when they are exploited, that is from December to May.

Our knowledge of reproduction at the population level will be limited from the onset by the lack of information concerning the situation of large cuttlefish from May to November.

4.3.3 Evolution of indexes

It should be noted from the start that large females (over 22 cm) are not available from June to November.

4.3.3.1 Percentages of maturing or ripe females: The monthly percentages of adult females in maturing or ripe conditions were calculated for all individuals from 13 cm to 22 cm (small and medium-sized cuttlefish) and for those of more than 22 cm (large cuttlefish).

We have chosen to stratify our adult cuttlefish samples into those over and those under 22 cm for reasons indicated above.

The proportion of small and medium-sized females in maturing conditions (Figure 23) is low from November to March and high from April to October. The one for large cuttlefish is consistently high during the period when they are caught, that is from December to May. For small and medium-sized mature females, the proportions are higher from April to September, and for the large ones in February-May (Figure 24).

4.3.3.2 GSR and NSR: Monthly average GSR indexes were calculated for the two size classes defined above from 1977 to 1979 (Figure 25).

The NSR were calculated in the same way for 1979 (Figure 26). A few gaps can be seen due to the absence of samples of large cuttlefish in 1977, and the absence of samples of small and medium-sized cuttlefish in November 1977 and October 1978.

In the group of the small and medium-sized we observe a high GSR peak from April to June and a secondary peak in August of each year. After May, the index begins to drop. On the other hand, for the large individuals, the GSR is high during the period when they are captured, with a decrease (less marked than for the smaller sizes) in February-March.

For small and medium-sized individuals the NSR develops simultaneously with the GSR, with a main maximum in April-June and a secondary one in August. Among the large cuttlefish, the only difference found between GSR and NSR variations was observed in February when a maximum GSR and a minimum NSR were found. This might be due to the accumulation of cuttlefish in trawls or transport vans which in the case of mature individuals could cause an emission of nidamental secretion. In fact large females have relatively larger nidamental glands than small females and could be more subject to losses of glandular substance at the time of spawning, that is, in February.

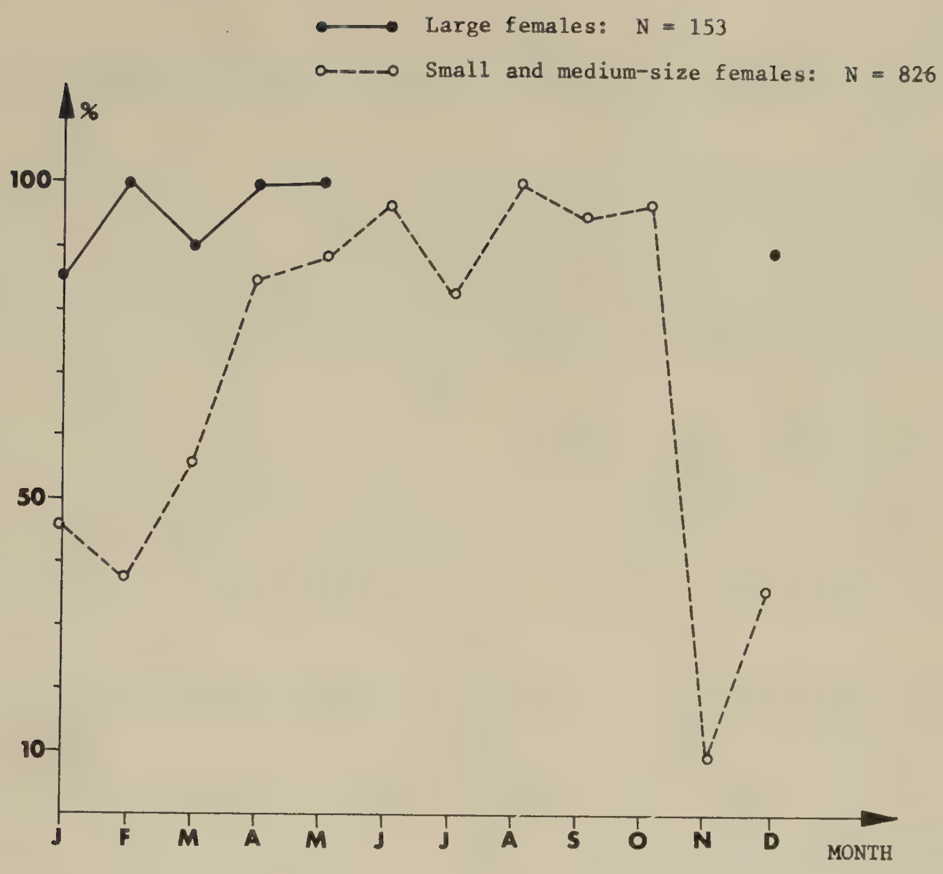


Figure 23 Evolution of ratios of adult females in maturation stage by size class

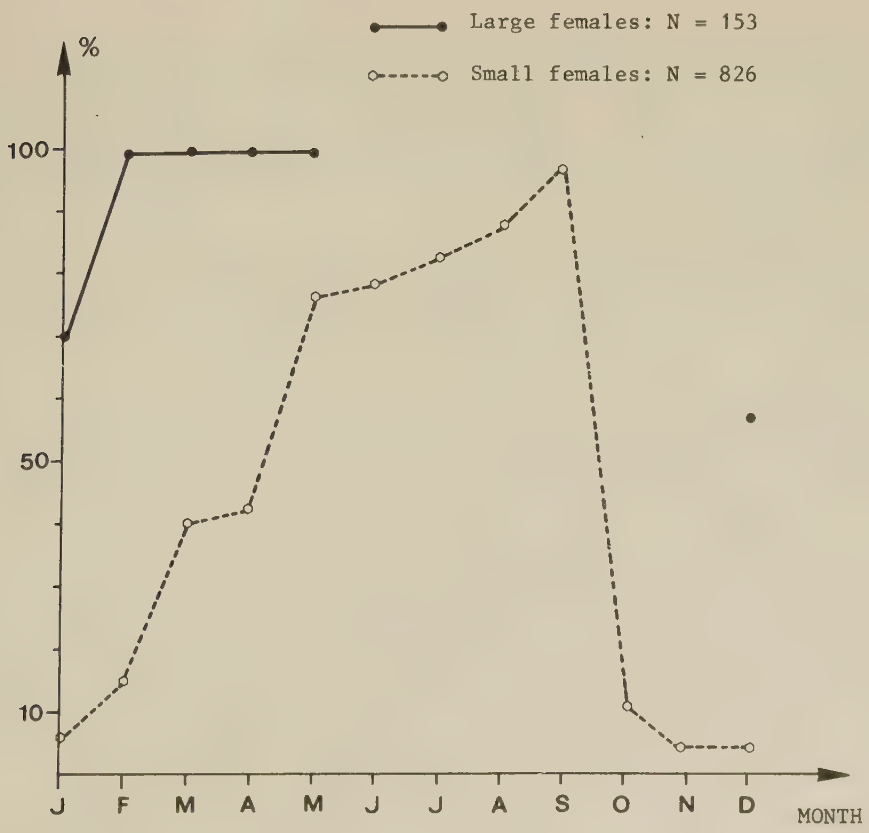


Figure 24 Evolution of mature female ratios by size class

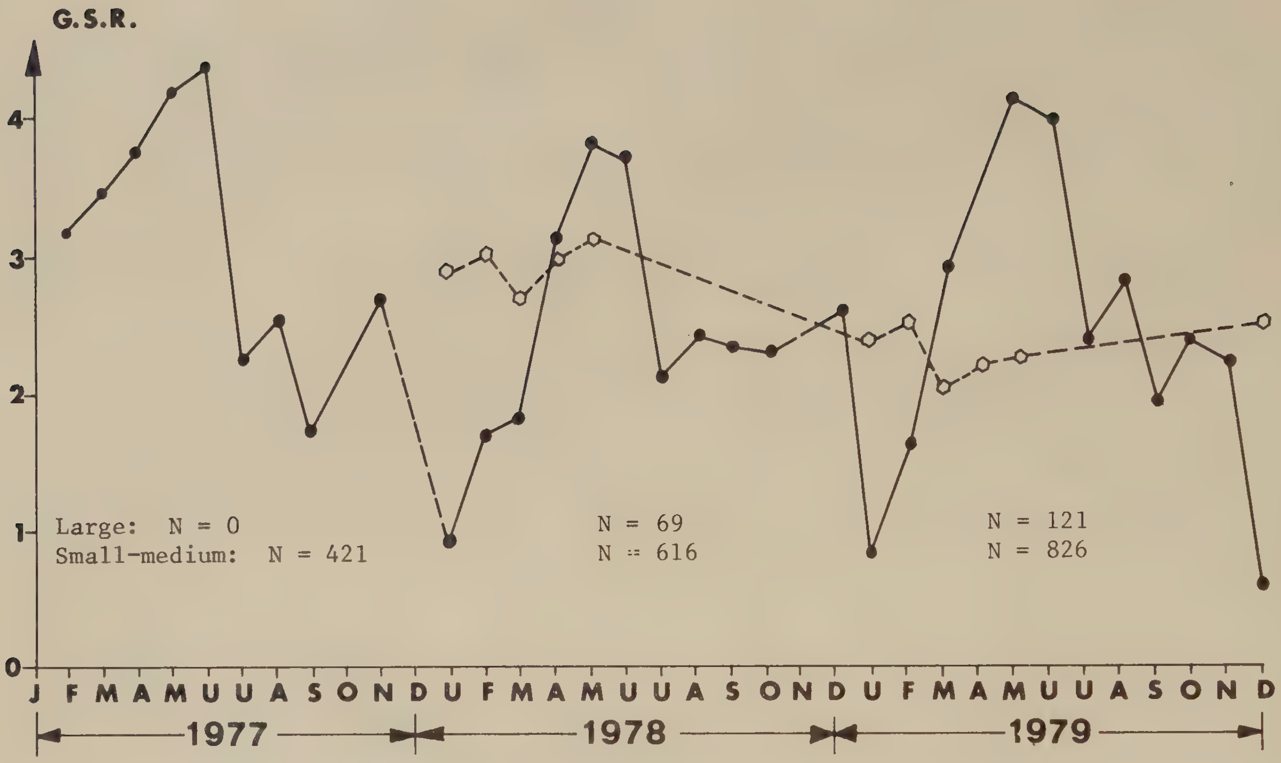


Figure 25 Evolution of monthly average Gonado-somatic ratio (GSR) by size category from 1977 to 1979

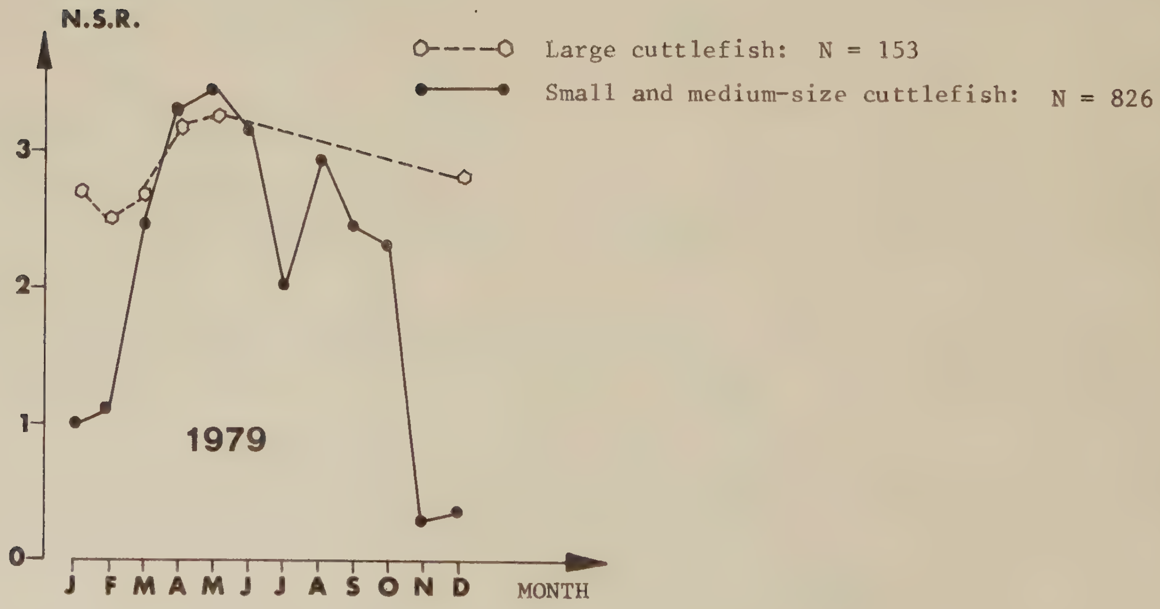


Figure 26 Evolution of Nidamental-somatic ratio (NSR) monthly average by size class, 1979

NOTE: Large cuttlefish are over 22 cm. Small and medium-size cuttlefish from 13 to 22 cm

4.3.3.3 Note on spawning abundance: Spawning abundance on the fishing grounds was not studied as thoroughly as the other reproduction indexes. We only have qualitative data from trawling and from observations on traps and purse seine nets.

Trawling data. We retrieved cuttlefish spawn in the trawl of the vessel LAURENT AMARO in April-May and September 1979. Our March 1980 campaign also enabled us to retrieve spawn. The samples taken from these spawning grounds showed that large cuttlefish were maturer sexually and had reached stage 4. Therefore they were probably responsible for the spawn. It should be mentioned however, that the quantity of spawn collected was small. Our surveys among fishing skippers show that cuttlefish eggs were found on fishing grounds in February-May and August-September. The most frequent and abundant spawn retrievals by trawls seem to occur from March to May. Another less marked period is August-September.

Trap fishing data. Traps serve as support for cuttlefish spawn. The cuttlefish come to them to attach their eggs during the spawning season and are caught. The St. Louis, Bel Air and Joal fishing grounds are those used most by the artisanal fishermen for trap fishing. The gear is put down on those grounds respectively from March to August, all year long and from March to July. During those periods spawn is observed there. It seems to be most abundant at St. Louis from May to August, at Bel Air from January to May and in August-September, and at Joal from April to May. During these trap-fishing periods eggs are also found in the gillnets of the artisanal fishermen.

It appears therefore that cuttlefish spawn all year long, with periods of high intensity from February to May and in August-September.

4.3.3.4 Interpretation of the results: The results which we have just described should be analysed taking into account cuttlefish migrations and the fact that females in the post-spawning stage are seldom observed. According to the findings, cuttlefish on the Senegalese coasts show permanent sexual activity. The proportion of mature females is never nil and spawn is found on the fishing grounds throughout the year. The GSR and NSR, abundance of mature females and spawning peaks are observed at the times when waves of cuttlefish move inshore. The minimum activity periods coincide with the periods when they remain offshore.

Consequently, it seems that the periods most favourable to the reproduction of small and medium-sized cuttlefish are March-June and August-September. These periods correspond to those when individuals of these categories are most abundant. At the same time they coincide with the periods of high spawning intensity. Small and medium-sized individuals come inshore to spawn in two waves from March to June and August-September and then withdraw offshore. Spawning is more intense in the first period because these cuttlefish are more abundant at that time.

Large cuttlefish reproduce in the course of their migration cycle when they stay in the inshore waters in February-March. We believe that, like the smaller sized categories, they do not reproduce from June to November when they return to deep water where they are inaccessible.

In short, the intense cuttlefish spawning periods are from February to June and to a lesser extent from August to September. There are variations according to size: large individuals spawn earlier in February-March, and a large majority of the small and medium-sized ones spawn from April to June and then from August to September.

These conclusions are confirmed by other authors. Garcia Cabrera (1968) reports that on the coasts of the western Sahara mature cuttlefish of the same subspecies are abundant from January to May and in July-August. Mangold (1963) notes that the Mediterranena *Sepia officinalis officinalis* spawn all year long with a clear maximum from April to July; the large cuttlefish spawn first in April, followed by the medium-sized and small ones from May to July.

4.4 Fecundity

4.4.1 Definitions

The term fecundity has received a number of definitions (Bagenal 1973). We shall adopt those that allow us to estimate reproduction capacity and the theoretical fecundity used in population dynamics. We mention the following:

(a) The individual partial fecundity (Fontana 1969) or the number of larger ovocytes in the ovary at the pre-spawning stage. Multiplied by the number of spawnings, this gives the total individual fecundity;
(b) The individual relative fecundity, corresponding to the individual partial or total fecundity divided by body weight;
(c) The reproductive capacity or global fecundity of the population, integrating the partial or total individual fecundity, the size structure of the exploited stock, the sex ratio, the average size at first maturity, and even the abundance (or an abundance index). This concept was introduced by Fontana (1979);
(d) The theoretical fecundity (Le Guèn 1971). This term denotes the total partial fecundity of an age class throughout its life. It is comparable to the theoretical fecundity of the total population at a given time, assuming that the population is in equilibrium and its recruitment constant. We shall not calculate this type of fecundity which requires a knowledge of the age structure of the population.

4.4.2 Methods

At stage 3, the gonads were removed whole and placed in jars containing water. The large reticulated and smooth eggs were counted within 12 h. Seventy-eight females of all sizes from 13 to 37 cm were studied in this way. Individual partial fecundity based on size (Figure 28) and individual relative fecundity were then calculated before estimating the total annual fecundity. After this the sex ratio by size class was obtained from 5 356 individuals trawled during our March 1980 campaign (Figure 27). At the same time, the structure by size class was estimated for the total catches by extrapolating the monthly frequencies per commercial category of the industrial and artisanal catches. Frequencies thus obtained by type of fishery were added up per 1-cm size class (Figure 29).

These data enabled us to estimate the egg production capacity C:

$$C = S_t \times S_{ra} \times F_t$$

S_t = catch size structure; S_{ra} = sex ratio; F_t = fecundity according to size

4.4.3 Results and discussion

4.4.3.1 Individual partial and relative fecundity: Figure 28 shows the evolution of the individual partial fecundity with size. The point cluster yielded a curve of the following equation:

$$Fe = 2.59 \; L^{1.77}$$

where Fe = fecundity and L is size in cm.

At the time of spawning, the fecundity varies from 250 eggs for 13 cm females to 1 400 eggs for those of 35 cm.

The average individual relative fecundity calculated for all sizes is 0.52 eggs/g. Ikeda *et al.* (1976), estimated the fecundity to be 50-300 eggs/female. However, as an index of fecundity they used the average number of eggs per cluster gathered by the trawl. We believe that our results are different from theirs because of the breaking up of the clusters. They are nevertheless close to those of Mangold (1963) whose counts of mature eggs are as follows:

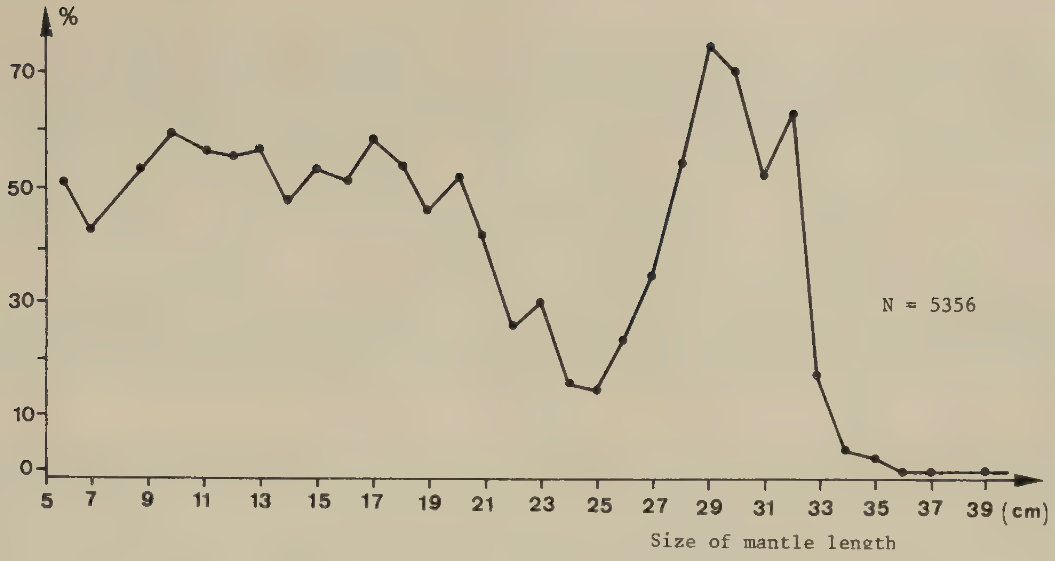


Figure 27 Sex ratio (% of females) according to size

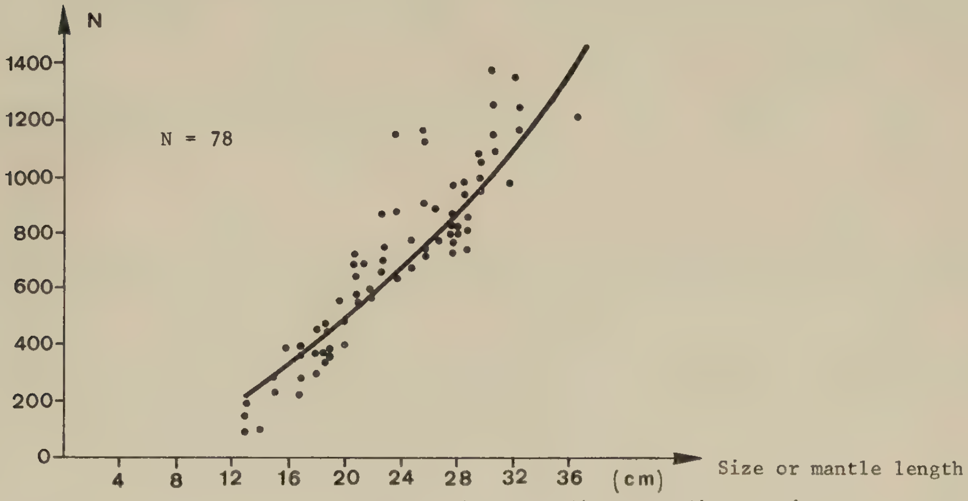


Figure 28 Evolution of individual partial fecundity according to size

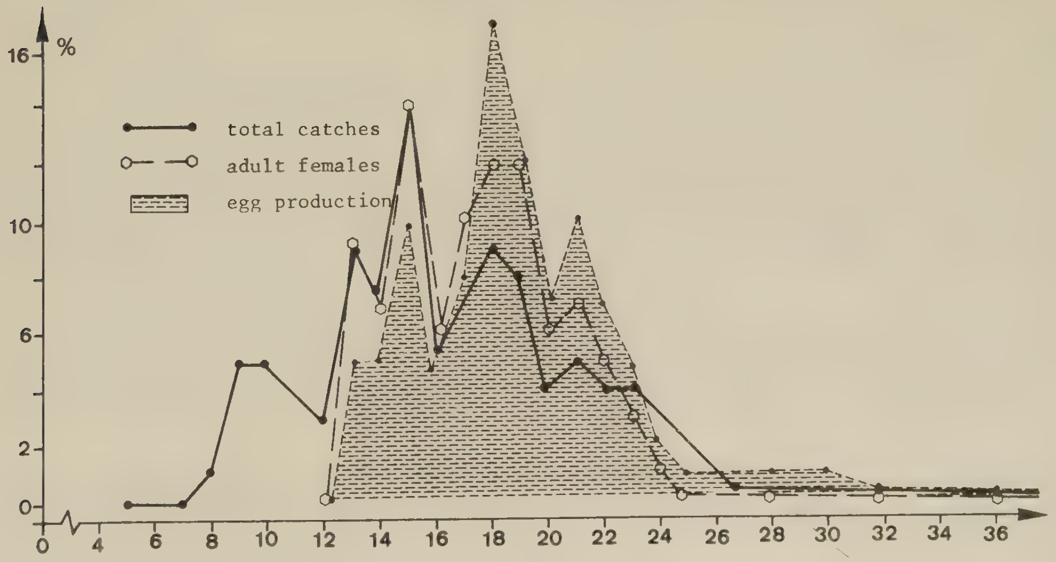


Figure 29 Relative proportion by size of:
- total catches (females + males)
- total catches of adult females
- egg production

Size (mm)		232	191	179	172	160	150	147	144	143	133	112
Fecundity	Mangold	550	480	460	375	355	235	225	275	215	135	160
	this study	676	479	427	398	350	312	301	290	287	252	-

Compared to fish that spawn millions of eggs, *Sepia officinalis hierredda* is a low fecundity species. Consequently, it cannot support a high exploitation rate and has difficulty in dampening the interannual recruitment variations because of its stock: recruitment ratio which should be practically 1:1 (Cushing 1975).

4.4.3.2 Individual total fecundity: This magnitude can be obtained by multiplying the individual partial fecundity by the number of spawnings per year. The first factor is studied above, the number of annual spawnings is unknown. We have shown that cuttlefish reach sexual maturity in offshore waters, come inshore to spawn and withdraw again in deep waters. This cycle takes place once a year and the duration of the stay in inshore waters is brief; the large individuals which begin to arrive in January have practically disappeared by April.

During their stay in the well lit inshore waters that block maturation and provoke spawning (Richard and Lemaire 1975), the development of small and medium-sized eggs is probably arrested until the next migration to deep waters. Large cuttlefish come to the spawning grounds only once a year; we suppose that this applies to the small and medium-sized ones as well.

Therefore it seems probable that a cuttlefish spawns once a year. Individual total fecundity would thus be the same as individual partial fecundity.

4.4.3.3 Reproduction capacity: Figure 29 indicates that cuttlefish of 13-24 cm long form the major part of the spawning stock. Juveniles participate relatively little in spawning, but are important in the catches. Consequently, the exploitation method could affect the survival of the stock. Since fecundity is low as well, it would be advisable to increase the mesh size used (55 mm) at least to the level of that authorized by fishery regulations (70 mm) until proposals can be made based on studies of selectivity and size at first maturity taking into account the reproduction capacity.

4.5 Spawning Areas

A knowledge of spawning areas, like that of the spawning seasons, could be obtained through trawling campaigns and surveys among fishermen: the LAURENT AMARO trawling campaigns enabled us to retrieve cuttlefish eggs in front of Joal on 10-15 m deep fishing grounds in April-May and in September. No eggs were trawled during our February 1979 campaign with pair-trawlers on the grounds of M'Bour and Sangomar. On the other hand, eggs were fished in front of Joal between 10 and 14 m depth during the March 1980 campaign.

On the basis of surveys among fishing skippers, it seems that trawlers gather cuttlefish eggs only on the Petite Côte and in Casamance, mainly on grounds of 12-14 m and 18-25 m respectively. The grounds in front of Saloum and Casamance in particular, as well as those south of Casamance, appear to be preferred spawning areas.

Fishery data indicate that trap-fishing is practised on grounds where females come to seek supports for attaching their eggs, that is, on the shallow grounds of the Petite Côte and in front of St. Louis. The gillnets set on shallow grounds also retrieve eggs.

From all these observations we conclude that cuttlefish come inshore to spawn. In fact it is on shallow grounds that they are likely to find supports to attach their eggs. This is why grounds with grasses and macrophyte algae and the river mouths of the Senegalese coast are spawning areas. Garcia Cabrera (1968) and Mangold (1963) observed the same behaviour among the cuttlefish of the western Sahara and the Mediterranean.

This would also seem to be general among all cephalopods. Mangold (1963) observed this among three other cephalopod groups (cuttlefish, octopus and squid) in the Mediterranean, Guerra (1979) among *Octopus vulgaris* in the western Sahara, and Worms (1979a) among *Loligo vulgaris* in the Mediterranean.

4.6 Factors Determining Gonad Maturation and Spawning

The influence of external and internal factors on gonad maturation and spawning in cephalopods has been studied by many authors, including Richard (1966, 1967, 1968, 1969, 1970, 1971, 1972a), Wells and Wells (1959, 1969, 1972), Mangold (1963), Boletzky *et al.* (1971), Mangold and Boucher Rodoni (1973), Rowe and Mangold (1975), Mangold *et al.* (1975), Richard and Lemaire (1975), Mangold and Froesch (1977).

The results of these studies indicate that fasting provokes sexual maturation in the squid species, *Illex illecebrosus* and in the octopus, *Eledone cirrosa*, but has no influence on that of several *Sepiola* and *Sepietta*. In *Sepia officinalis*, diet, temperature and salinity also seem to have no influence on maturation and spawning. On the other hand, darkness accelerates maturation and inhibits spawning, whereas prolonged or intense light inhibits maturation and provokes spawning (light influences reproduction only in adult females). Richard and Lemaire (1975) explain this phenomenon by a neuro-hormonal light mechanism that affects the gonad. The light signal received by the eye is transmitted to the brain which reflects it on the optical gland. Hormones secreted by that gland affect the gonad. A feed-back mechanism may inhibit genital maturation when external conditions are unfavourable to reproduction (Richard (1970).

In the case of the Senegalese cuttlefish, temperature does not seem to influence reproduction in the large individuals. In juveniles, we find a uniform pattern all along the African coasts (FAO 1978) with a main spawning period when the waters become warmer; however, in the present case, contrary to the general findings, secondary spawning occurs at the height of the warm season. Light seems to be a more important factor: large cuttlefish undergo their sexual maturation during their stay in deep waters from June to November, and small and medium-sized ones from October to February. The return inshore when the grounds are well lighted probably inhibits maturation and triggers spawning in adult individuals. The combined effect of the migration cycle and lighting are therefore the most probable factors conditioning the sexual cycle.

Conclusion. The female of *S. officinalis hierredda* of the Senegalese coasts is mature at a size of 13 cm. During the stay in deep waters where light is absent, she undergoes sexual maturation, then migrates inshore where she finds both the light which triggers spawning and arrests maturation completely and the supports to attach her eggs. She then returns to deep grounds and the cycle starts over again.

5. BIOMETRY AND GROWTH

A biometric study might have shown whether the cuttlefish of Casamance are different from those of the Petite Côte. As samples from these areas were not available, this aspect could not be included in the present study. On the other hand, biometric criteria for distinguishing *Sepia officinalis hierredda* from *Sepia officinalis officinalis* and *Sepia officinalis vermiculata* could be established.

The study of growth is fundamental for the models of rational management which we will have to use.

5.1 Biometry

The reason for a biometric study of cuttlefish has been mentioned previously. In addition, the selection of parameters will be discussed in the present introduction.

The hard parts having the least variability, that is cuttlebone and beak, were measured. The mantle was also studied, but fresh in order to reduce variations connected with the decomposition of the animals. The systematic scope of this study led us to consider the dimensions studied by Adam (1941), Clarke (1962) and Mangold and Fioroni (1966): cuttlebone (or dorsal mantle) length, cuttlebone width, length of hood and ridge of each beak, open mantle width. These parameters seem to constitute systematic criteria.

Adam (1941) distinguishes the two 'subspecies' of *Sepia officinalis* found south of Cape Blanc by the relative width and thickness of their cuttlebones. We have not studied this second dimension because of the regeneration and degeneration processes occurring in the shell epithelium, depending on the physiological condition of the cuttlefish (Mangold 1966); these phenomena are possibly responsible for the decreases of cuttlebone thickness that we observed during spawning periods, especially in females.

Clarke (1962) draws attention to the possibility of following the evolution of certain cephalopod families by comparing the beaks. Mangold and Fioroni (1966) point out that the jaws provide a "valuable means of identifying the species."

5.1.1 Data treatment and results

In each sex, we have studied the relation between: (a) length of the hood and ridge of each jaw; (b) cuttlebone length and width. As a regression line was used the small main axis or Teissier (1948) line. It is more appropriate in the case of a study of the allometric relationship. This type of fitting does not allow a comparison of the regression lines however. We have further studied: (c) the relation between mantle length and weight, as represented by the power function $W = aL^b$, for which the parameters were determined by fitting a Teissier line to the point cluster (values converted into Neperian logarithms for both sizes and weights). The different relations found are represented in Figures 30 to 38. Table 3 groups the number of couples measured, the correlation coefficients and the equations of the fitted lines.

5.1.2 Discussion

The value of the correlation coefficients (significant at the 5-percent level) confirms that regression lines can be fitted to our data other than those for the length-weight relationship. However, there seems to be a break in slope at the following lengths: 23-24 mm ridge length for females and 26 mm for males (Figures 32 and 33), 25 cm cuttlebone length for females and 28 cm for males (Figures 34 and 35). We do not know the cause of the first break. The second one could be connected with a change in biotope, since large cuttlefish live on deeper grounds from June to November. The fact that the break occurs at a greater length for males than for females could be a consequence of the more rapid growth of the former.

Females are relatively heavier than males (the confidence interval of the exponent b of the size/weight relation is calculated at a level of 5 percent, student's t test shows that this exponent differs significantly from 3 at this level). The size-weight relationship is also subject to some bias due to the fact that large cuttlefish are sampled only from December to May: the weight of large individuals, especially females, is sure to be overestimated at this period especially during the pre-spawning stage when the gonads are very large. On the other hand, some underestimation of the weight is found just after spawning when the gonads are spent and the animals are exhausted. Another problem is that the large cuttlefish having withdrawn to deeper waters than the juveniles in June-November, are not sampled during this period; however, even if samples were available, the difference in biotope would bias the size-weight relationship.

The exponent of the size-weight relationship found by us seems different from the one calculated by Guerra (1975) for *Sepia officinalis officinalis* of 23°-26°N: $P = 0.14L^{2.91}$ with a correlation coefficient of 0.94 and a length range of 5-35 cm for 1 076 males and females combined. This author's fitting was done by the least squares method.

Apart from the breakpoints in the slopes at different sizes according to sex and the relatively lighter weight of the males as compared to females, there seems to be no significant difference between males and females.

Our results also differ from those of Mangold (1966) and Clarke (1962) in slope and other constants (Table 4).

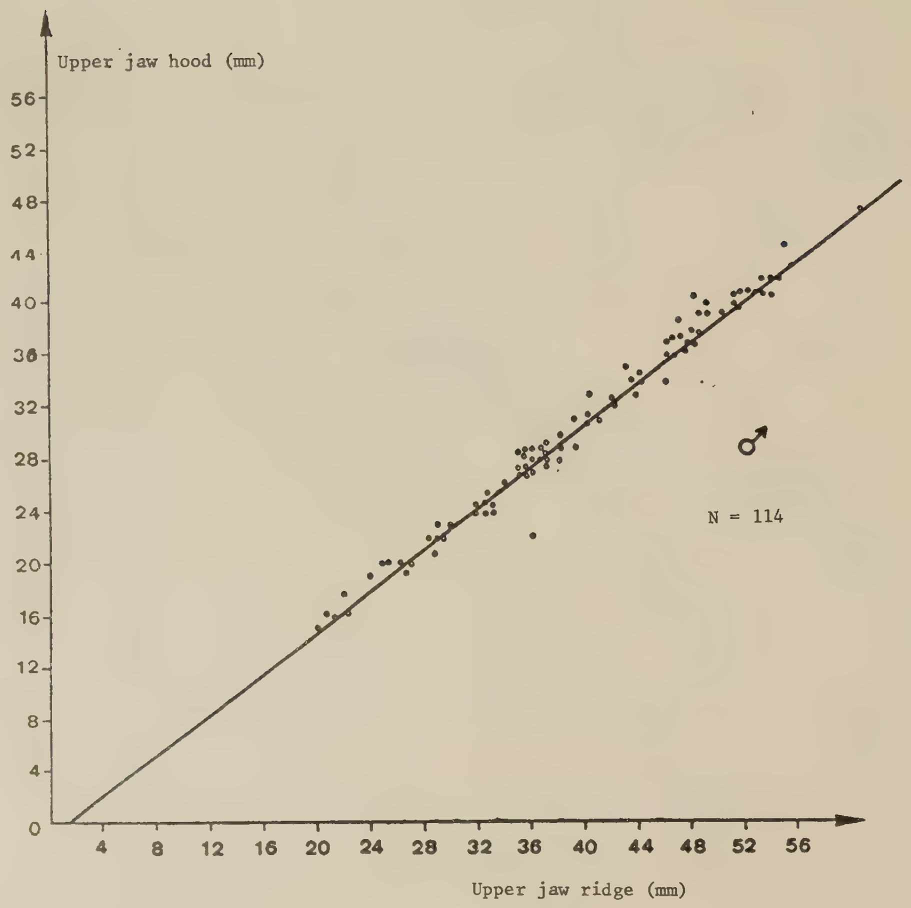


Figure 30 Relation between the lengths of upper jaw ridge and hood of male cuttlefish

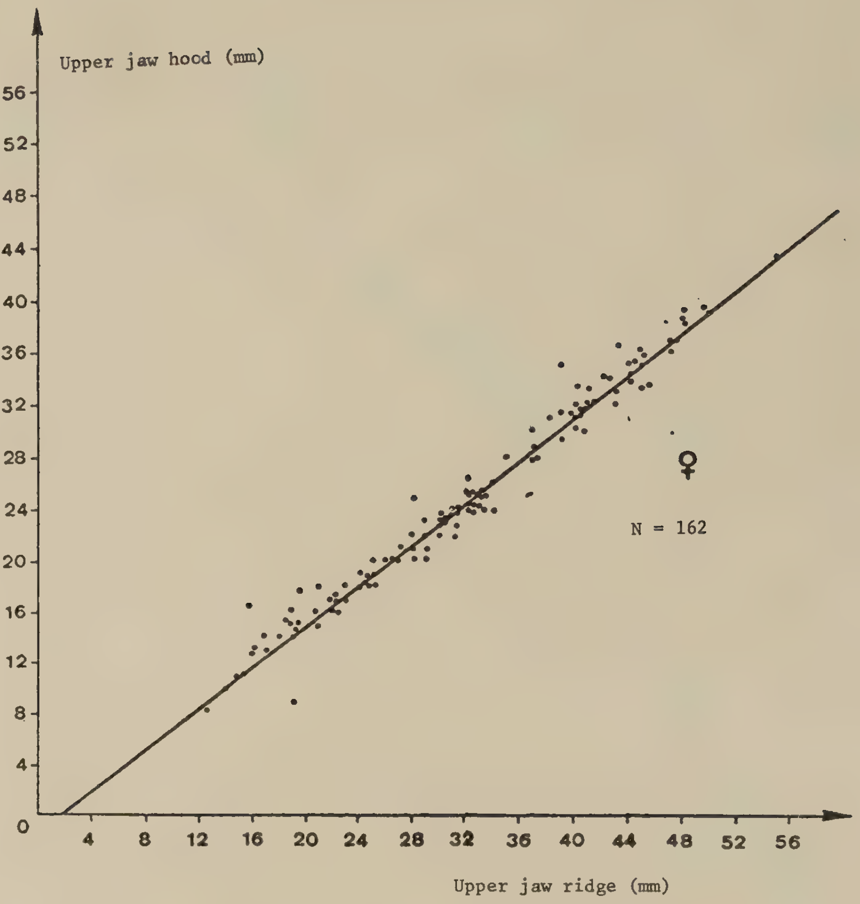


Figure 31 Relation between female upper jaw ridge and hood lengths

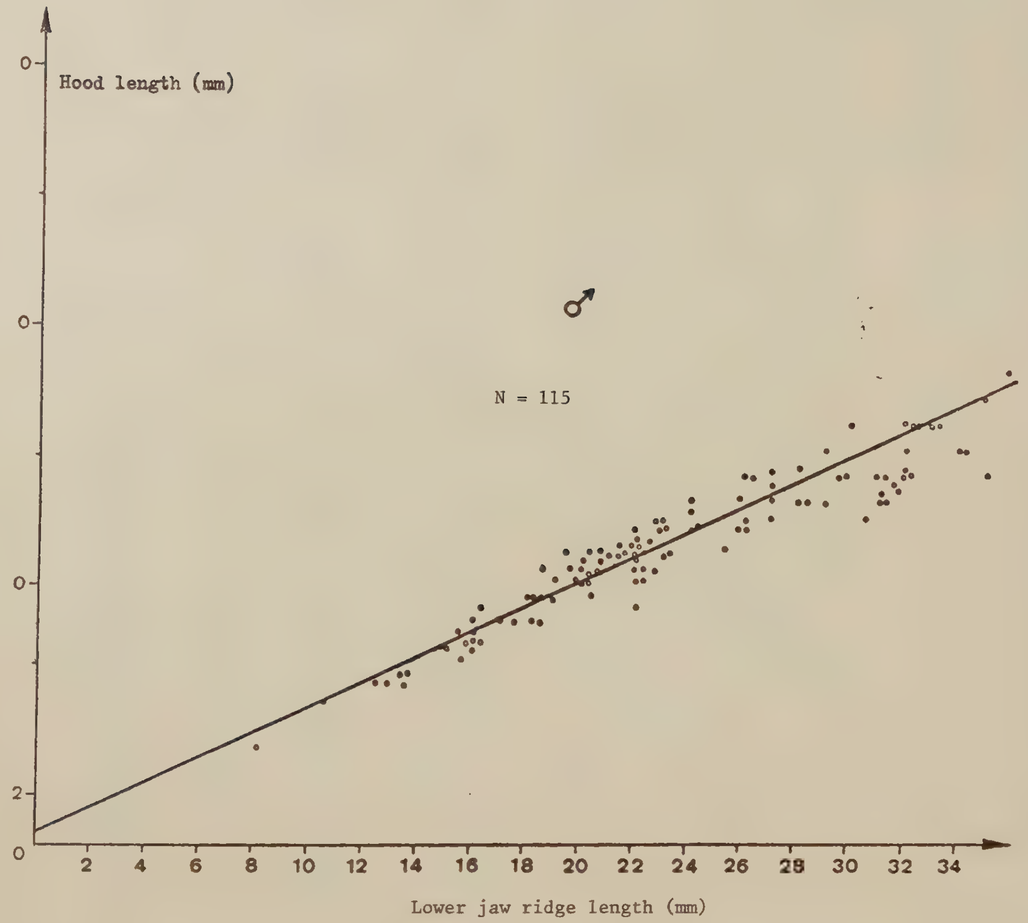


Figure 32 Relation between male lower jaw ridge and hood lengths

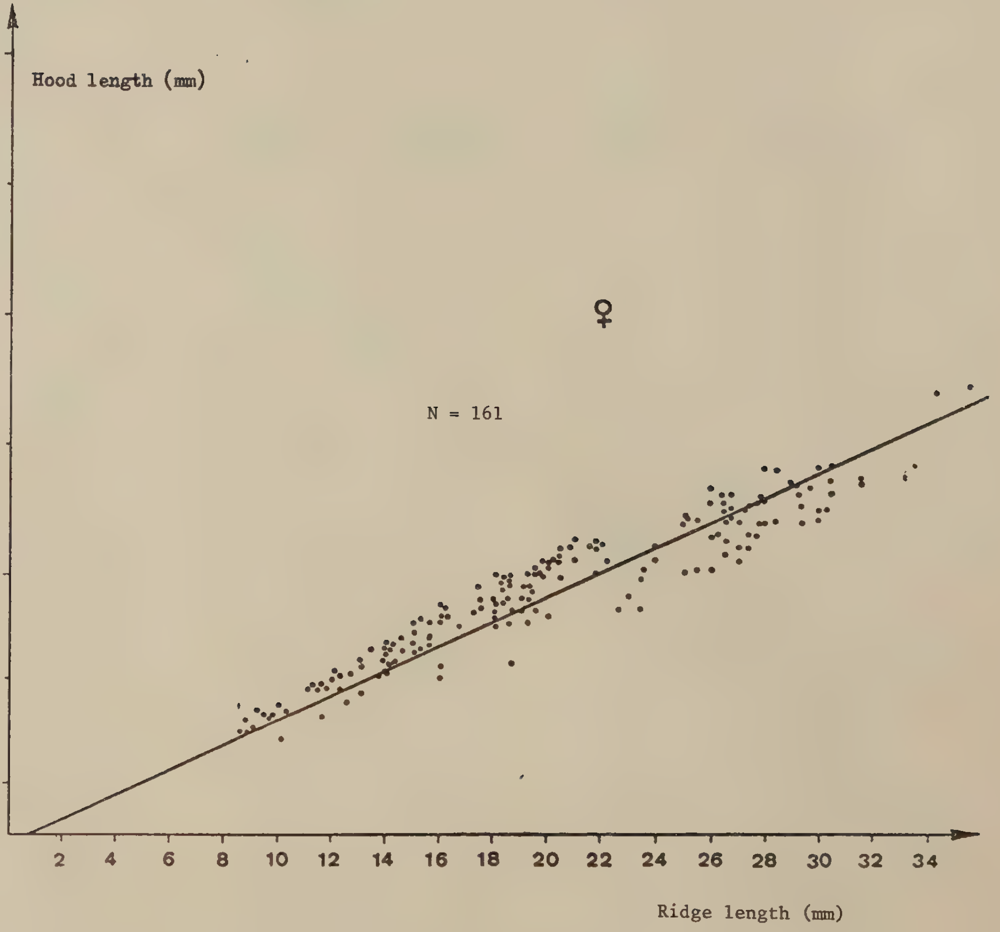


Figure 33 Relation between female lower jaw ridge and hood lengths

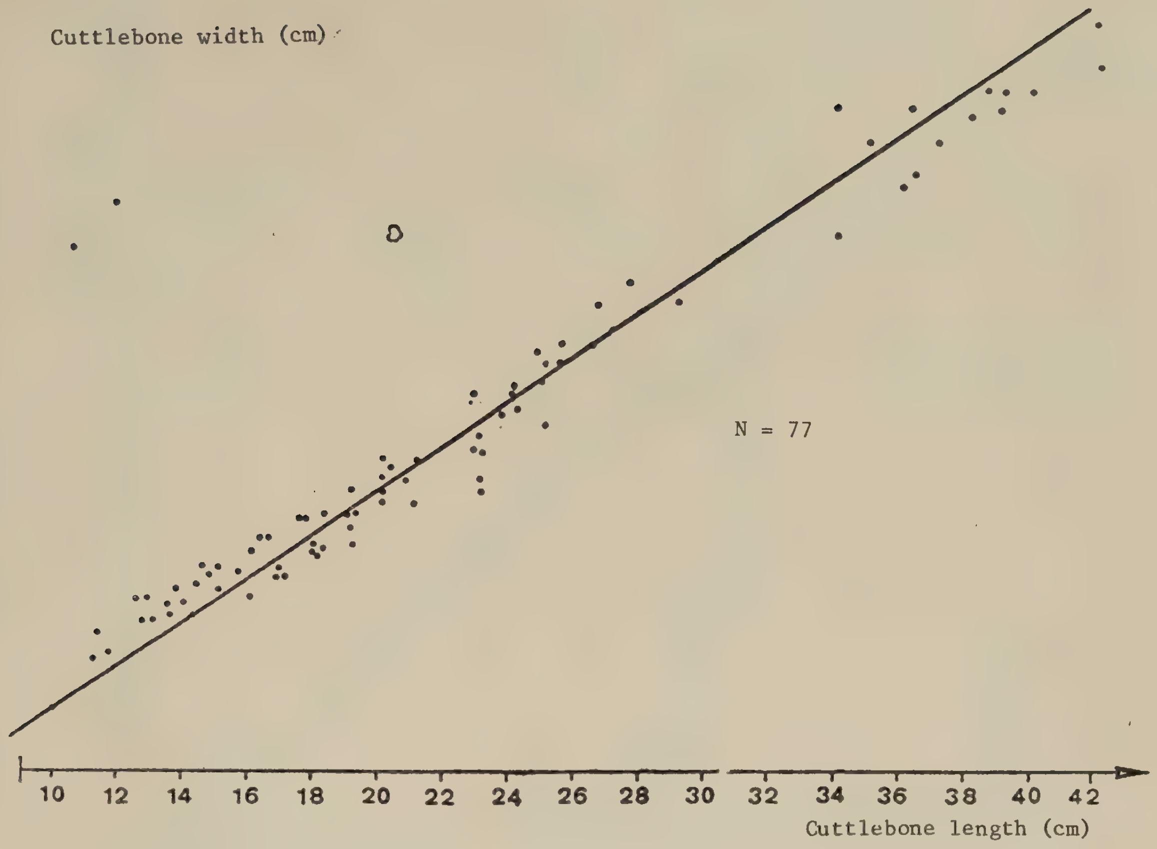


Figure 34 Relation between male cuttlebone length and width

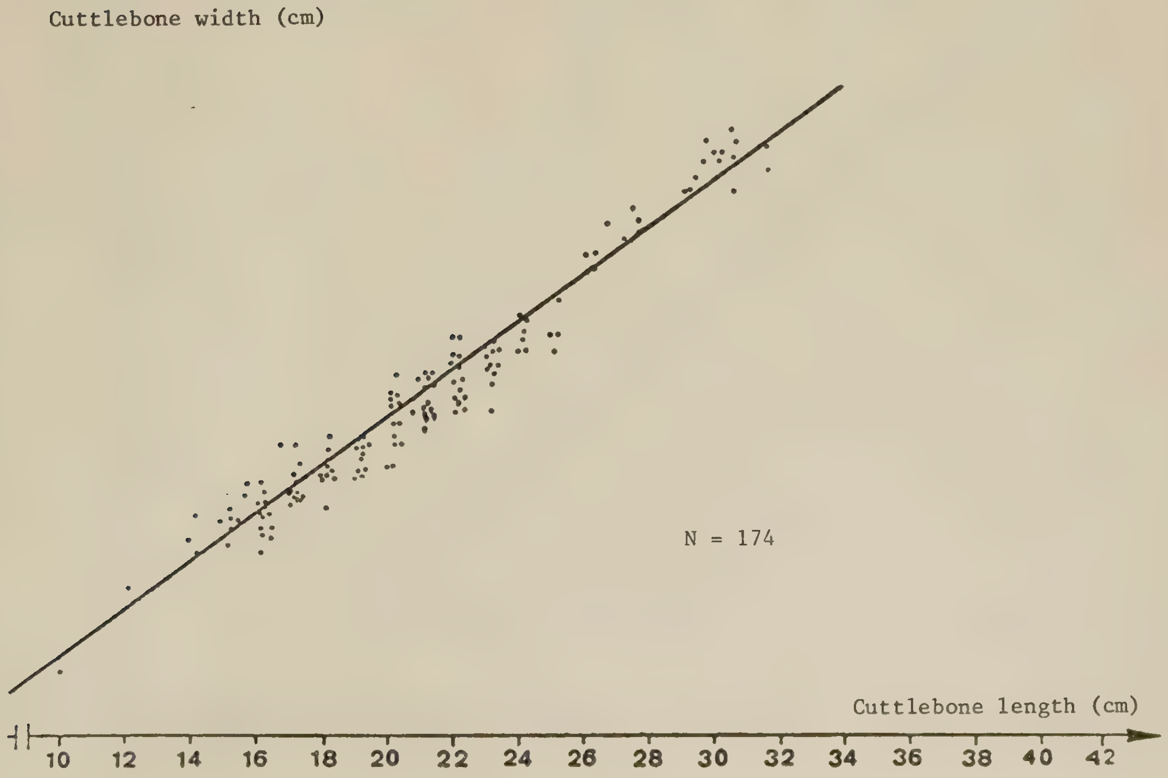


Figure 35 Relation between female cuttlebone length and width

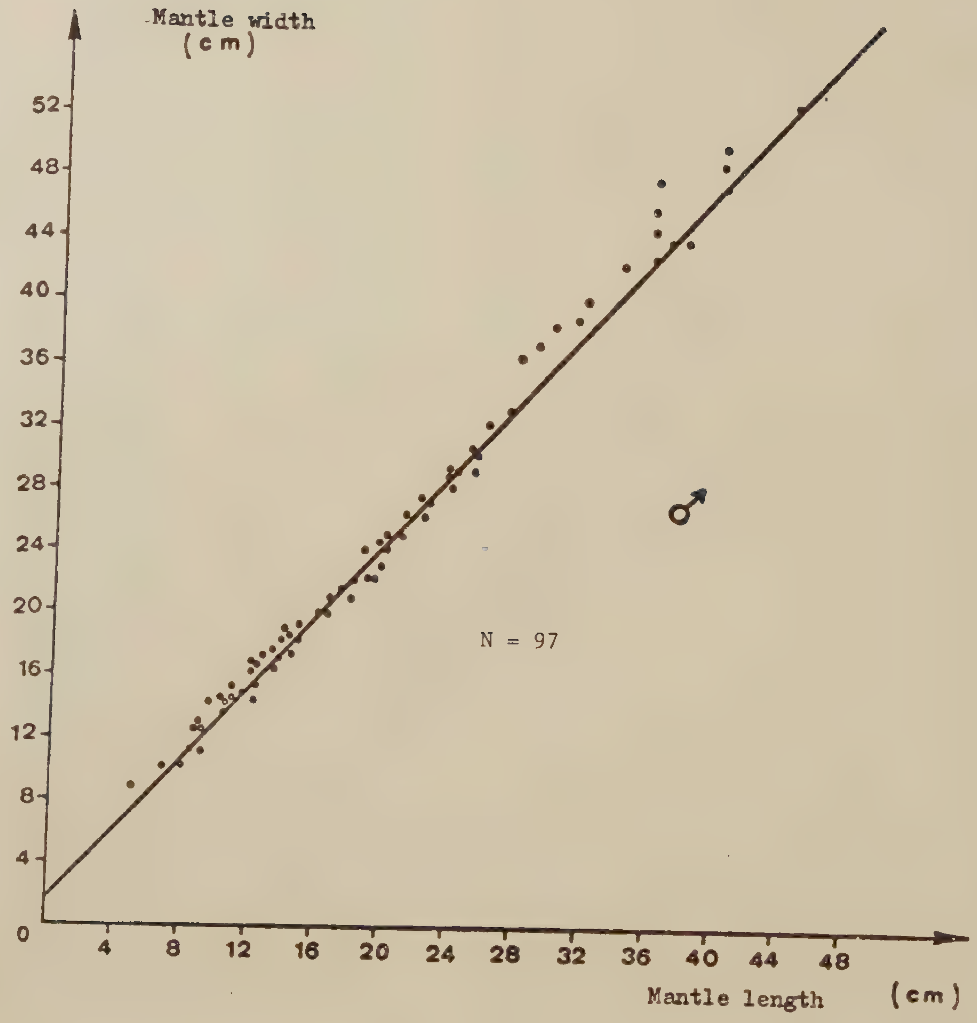


Figure 36 Relation between male mantle length and width

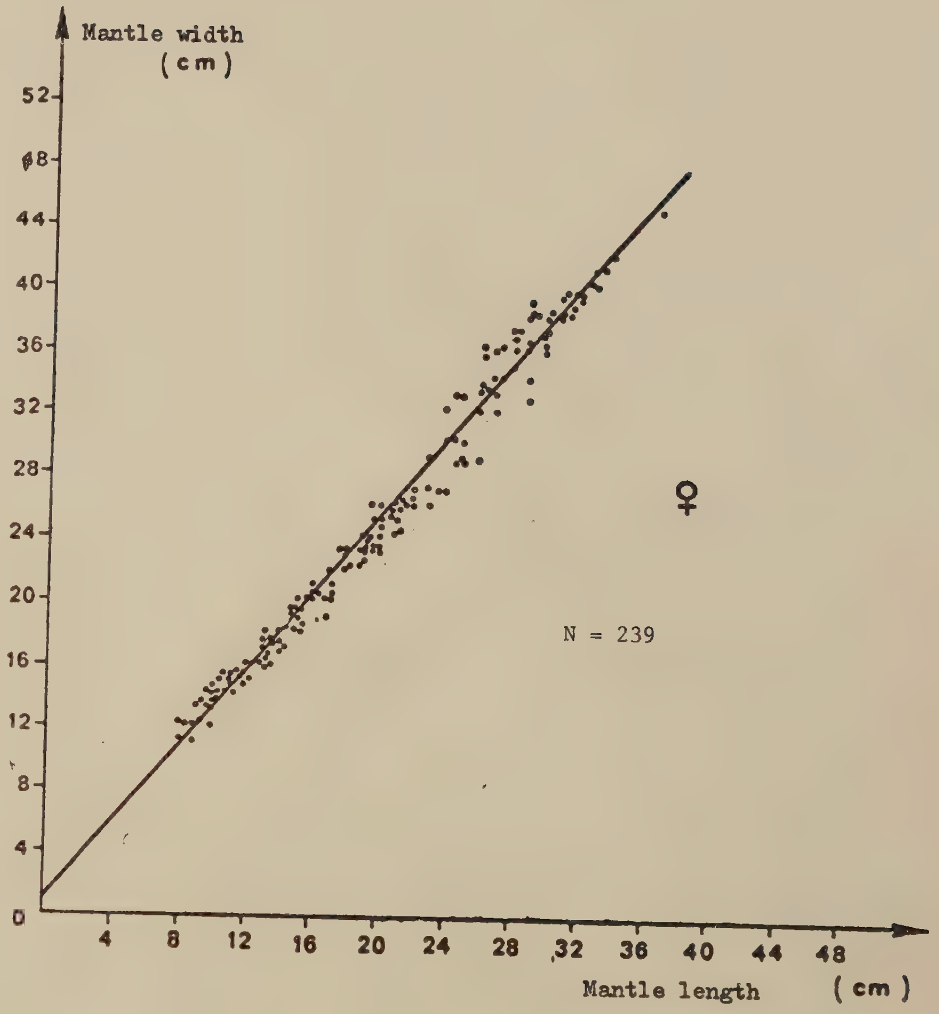


Figure 37 Relation between female mantle length and width

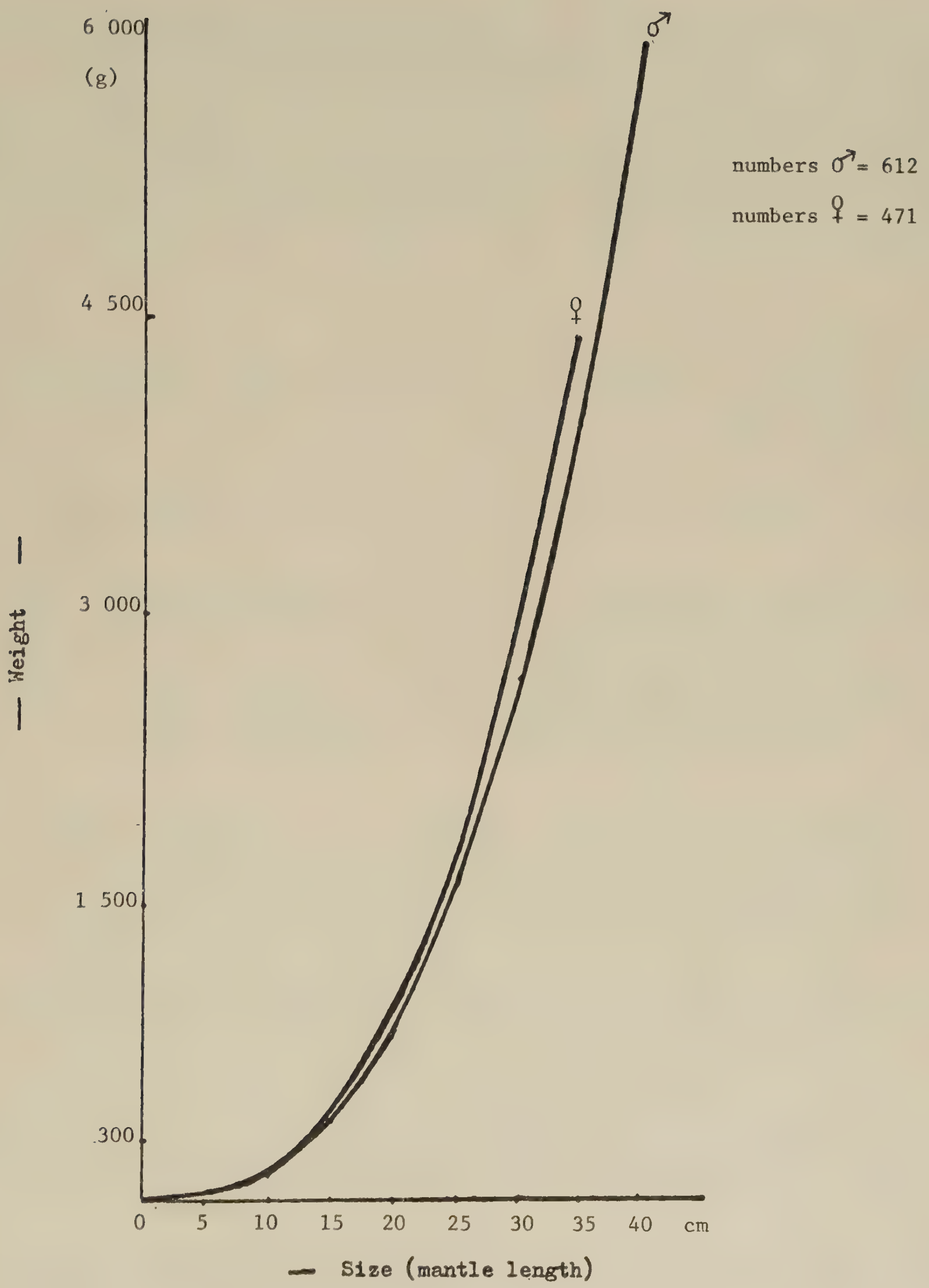


Figure 38 Cuttlefish size-weight ratio

Table 3

Parameters of fitted lines

		Number of couples	Correlation coefficients	Equations of lines fitted
Upper jaw (mm)	Males	114	0.98	$HL = 0.82\ RL - 1.44$
	Females	162	0.95	$HL = 0.82\ RL - 1.83$
Lower jaw (mm)	Males	115	0.93	$HL = 0.47\ RL + 0.54$
	Females	161	0.94	$HL = 0.45\ RL + 0.33$
Cuttlebone length and width (cm)	Males	77	0.96	$DL = 0.34\ CW - 0.43$
	Females	174	0.98	$DL = 0.38\ CW - 0.74$
Cuttlebone length and mantle width (cm)	Males	97	0.99	$DL = 1.16\ MW + 1.46$
	Females	239	0.99	$DL = 1.22\ MW + 0.59$
Mantle length (L) and weight (W)	Males	612 (5-44 cm)	0.99 (small main axis)	$W = 0.24\ L^{2.74\pm0.03}$
	Females	471 (7-37 cm)	0.99 (small main axis)	$W = 0.26\ L^{2.74\pm0.04}$

Abbreviations: HL = hood length
RL = ridge length
DL = dorsal mantle or cuttlebone length
CW = cuttlebone width
MW = mantle width

Table 4

Slopes and equilibrium constants (K) of Mangold (1966) and Clarke (1962)

		Slope	K acc. to Mangold	K acc. to Clarke
Upper jaw	Males	0.8	0.8	1.0
	Females	0.8	1.0	0.9
Lower jaw	Males	0.4	1.1	1.7
	Females	0.4	1.0	1.1

We do not know the number of couples that were used by Mangold and Clarke to establish the equilibrium constants nor the measurement range or the type of fitting they used. It is therefore difficult to compare our results with theirs. If, however, these authors worked the same way as we did, it must be recognized that *Sepia officinalis officinalis* is biometrically different from *Sepia officinalis hierredda*, especially as regards the relationship between hood and lower jaw ridge.

5.2 First Age and Growth Estimate of *Sepia officinalis hierredda* of the Senegalese Coasts

5.2.1 Previous studies

Not many studies have been made of the growth of Sepiidae. There are a few studies made in the laboratory by Richard (1966) and Boletzky (1974) and in natural conditions by Mangold (1963). These authors worked on *Sepia officinalis* of the European Atlantic and Mediterranean coasts. They measured dorsal mantle growth; cuttlefish age criteria were also sought. Choe (1963) believes that a stripe is formed on the cuttlebone every day. Adam (1941), Richard (1972), Yoshinobu, Takeshi and Masahara (1971) observed cuttlebone inter-stripe width differences which they related either to migration or reproduction. Therefore, the age could eventually be determined from knowledge of either the migration or the sexual cycles. Clarke (1965) observed stripes on the beak of the squid *Moroteuthis ingens* and believed that they could be used as age criteria, although he could not explain them.

5.2.2 Growth after recruitment in pair-trawler catches

5.2.2.1 Study method: Previous works have shown that cuttlefish growth could be examined using collective methods like that of Petersen and individual methods using age criteria. Consequently, we took size samples of dorsal mantle length or cuttlebone length, the beak and cuttlebone.

(a) Individual method - Age criteria could not be established based on beaks and cuttlebones. In fact, on the latter, as Adam (1941) pointed out, we did not observe any variation in inter-stripe width.

(b) Petersen's method - The Petersen method which we used assumes that a uniform modal progress during a constant time interval expresses the growth of an age class (or of a cohort). We should mention that the results of this method are more reliable for European species which spawn only once a year and therefore belong to only one age class. This does not apply to tropical areas where spawning is generally spread over a considerable time period or is even continuous. Consequently, the modal delimitations are highly subjective. They become even more difficult to examine when migration phenomena exist as in the case of cuttlefish.

This method was used after breakdown of the polymodal curves by the method of successive maximum recommended by Gheno and Le Guen (1968). The basic data consist of length frequencies for males by size classes of 2 cm in the pair-trawl landings. Because of the difficulty to define modes in histograms for females, we did not study the growth of the latter. The modal progressions are shown in Figure 39, while Figure 40 shows the resulting monthly average growth.

5.2.2.2 Results and discussion: Since the monthly growth rates deduced from the modal progressions are practically constant, we assume that a linear model of the form:

$$L_t = at + L^1_o \quad (L^1_o \text{ is the size at age } t^1_o)$$

fits the data. It should be noted however, that this model does not necessarily contradict the von Bertalanffy (1938) model generally used to represent growth; it should be kept in mind that we worked on relatively young animals whose growth corresponds to the rapid growth phase of von Bertalanffy's model.

For the model adopted we used the reduced main axis regression technique. Correlation coefficients (r) and the parameters a and L^1 were calculated and we obtained a growth equation for the length interval studied (Table 5).

The uniform modal progressions thus lead to results comparable to those of Mangold (1963) of 1.4 cm/month, taking into account temperature conditions in the Mediterranean and in Senegal. These results are also close to those of Richard (1966) who finds a linear growth of 1.85 cm/month for cuttlefish in the aquarium at 20°C.

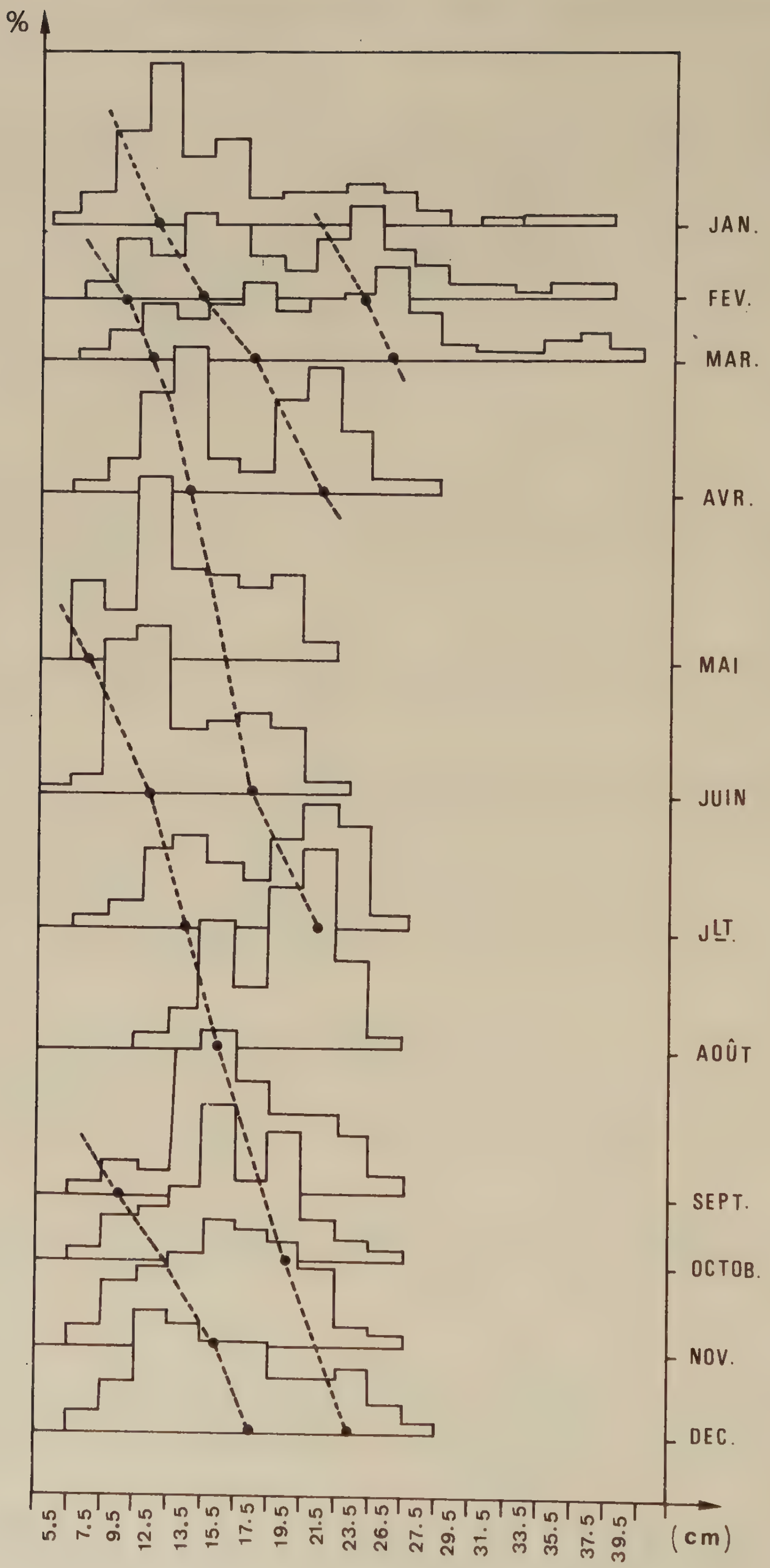


Figure 39 Male cuttlefish monthly size frequencies and modal progressions (1979)

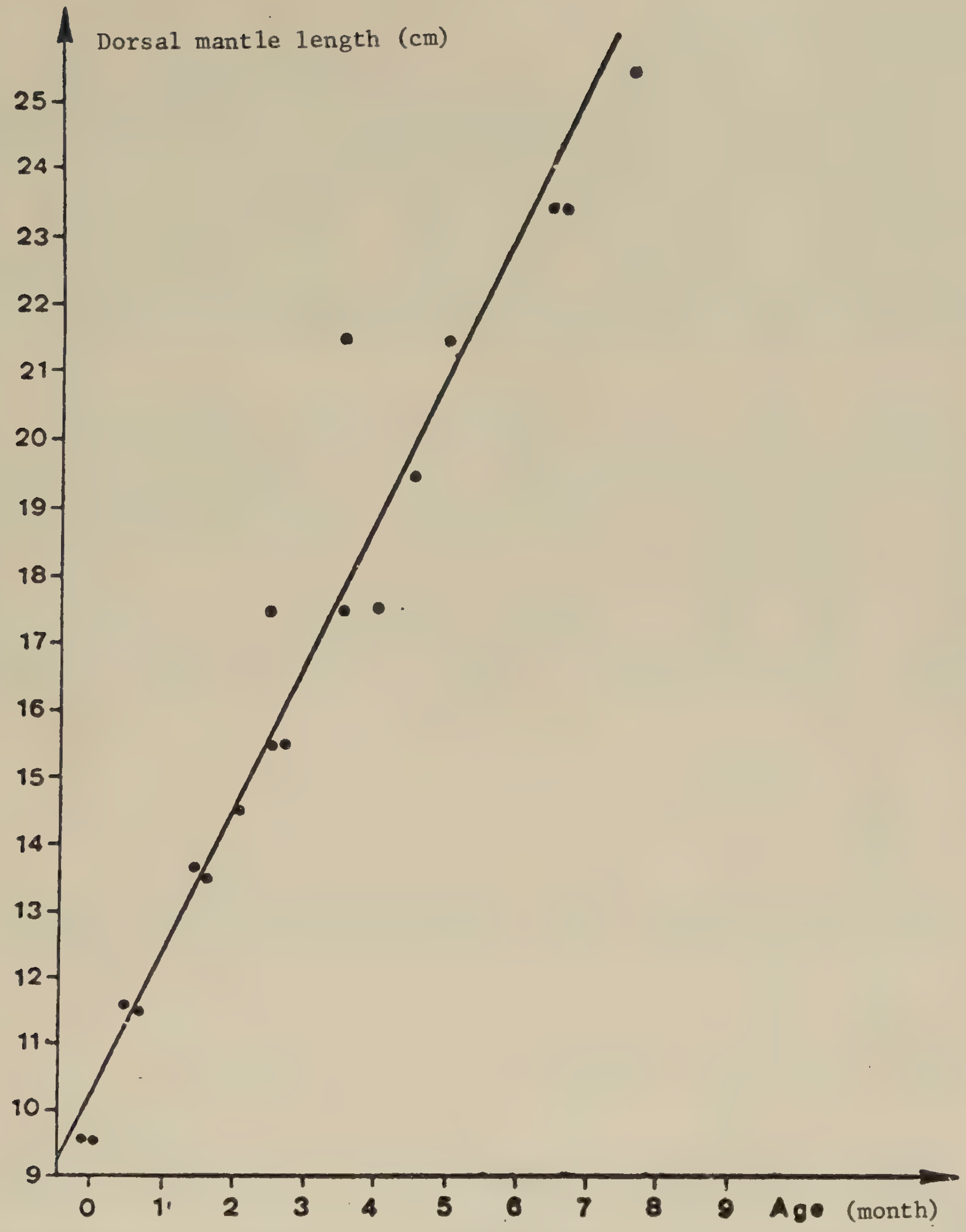


Figure 40 Male monthly average relative growth from size at recruitment to the size of 25 cm

Table 5

Parameters and the growth equation of male *Sepia officinalis hierredda*

L^1_o	a	r	Equation (t in months)	Size interval used in this study
10.10	2.16	0.97	2.16t + 10.10	9-25 cm

5.2.3 Growth before recruitment

We estimated the growth before recruitment to the catches, based on the known spawning times and the duration of the incubation: based on the variations in GSR and NSR we have shown that spawning takes place mainly in February, June and September. Mangold's (1963) laboratory studies showed that the duration of incubation of *Sepia officinalis* eggs, within acceptable temperature limits, is proportionally shorter as the water is warmer (Figure 41). We accept this scheme as valid in natural conditions for *Sepia officinalis hierredda* and shall estimate the duration of egg incubation in Senegalese waters at 40 days for the February spawnings and less than one month for those of May and September. In fact, during those spawning periods the waters are respectively 19°C, 22°C and 26°C. Therefore, hatching probably takes place in March, June and September.

The recruitment of category P cuttlefish takes place in January, June and September (Figure 42), when the modes are at 9, 11 and 11 cm, respectively. This is also visible on the length frequency histograms of Figure 39. If we accept that the January, June and September recruits come from the respective hatchings of September, March and June, their ages would be 3, 4 and 5 months. We shall assume, as Richard (1975) notes for the Mediterranean *Sepia officinalis*, that the size at hatching averages approximately 7 mm. Consequently, the growth rate seems to be 3 cm/month for the March recruits, 2.7 and 2.2 cm/month for those of June and September, respectively. The abundance of food during the cold season and the lack of it in the warm season (Touré 1972), illustrated in Figure 43, could explain this abnormal difference in growth of cohorts in their early months of life. The average growth rate resulting from these estimates for different cohorts is 2.6 cm/month.

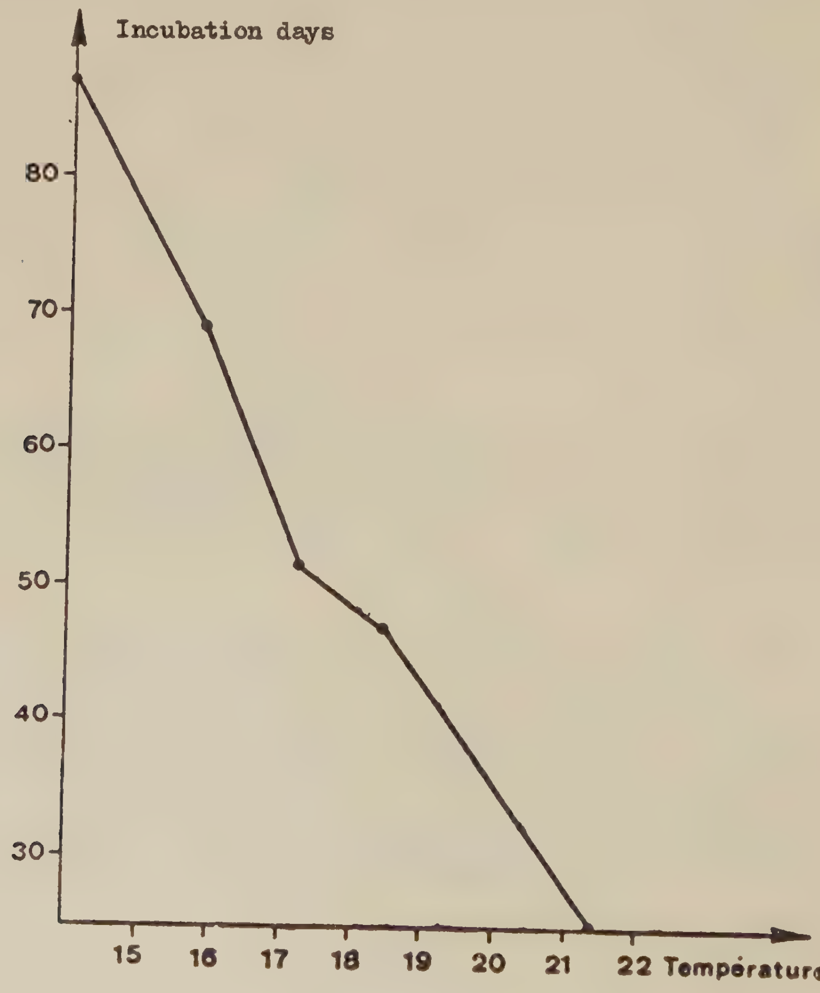


Figure 41 Influence of temperature on duration of incubation of *Sepia officinalis* eggs (Mangold 1963)

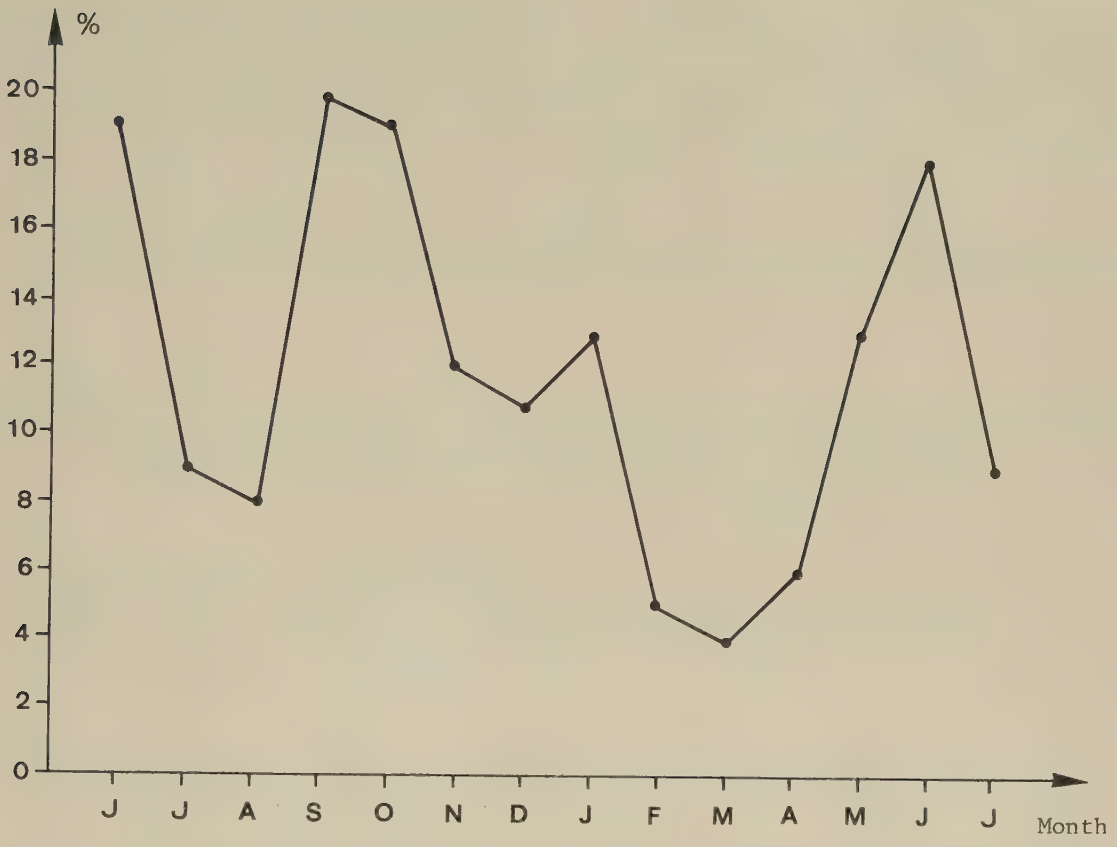


Figure 42 Monthly frequencies of commercial category P in trawl catches (June 1978-July 1979)

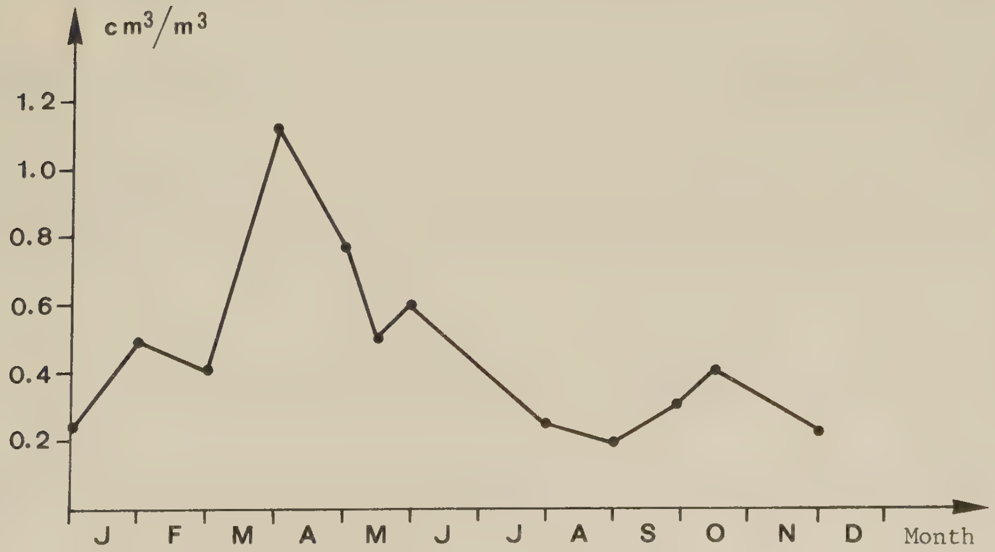


Figure 43 Average curve of monthly plankton volume variations on the Petite Côte of Senegal (Touré 1972)

5.2.4 Growth curves

5.2.4.1 Length growth: Growth from hatching to recruitment is represented by the equation $L = 2.6t + 0.7$, while the equation $L = 2.16t + 10.10$ expresses growth after recruitment up to 25 cm dorsal mantle length. Cuttlefish growth rates therefore seem to be very high and decrease progressively with age (Figure 44); complete cuttlebone growth should then be represented by a von Bertalanffy (1938) model which is an asymphotic negative exponential model.

5.2.4.2 Growth in weight: The weight growth equation, $W = 11.85t^{2.15}$, is the result of the size growth equation and the size-weight relationship. The curve representing it (Figure 45) shows a weight growth rate that increases with age during the first year.

5.2.5 Lifespan

A knowledge of the maximum age would be important, but this data is difficult to obtain for cephalopods, especially because of the lack of age criteria. Mangold (1963) believes that *Sepia officinalis officinalis* can reach four years of age in the Mediterranean. Kristensen (1959) thinks that these cuttlefish have a lifespan of at least two years in the Netherlands waters.

If we extrapolate the growth rate estimated above for *Sepia officinalis hierredda* of 9-25 cm to the maximum size (averaging 38 cm) observed for the species on the Senegalese coasts, this cuttlefish would reach a maximum lifespan of two years. Since growth is less rapid in older animals, the maximum age is probably more than two years.

5.2.6 Conclusions

This study on cuttlefish age and growth is far from complete. In fact, the age criteria we tried to establish on the basis of beak and cuttlebone were unsatisfactory.

The use of the Petersen method presents difficulties for a study of the growth of cephalopods with a short lifespan, a permanent recruitment with peak periods and migrations that make individuals of over 23-25 cm inaccessible to fishing gear during almost eight months of the year.

Other methods should be considered, especially a study of the statoliths, as these bony parts made it possible to establish the age of the squid *Illex illecebrosus* (Lipinski 1980). Tagging should also be tried.

The data we have analysed in this study justify nevertheless the assumption that *Sepia officinalis hierredda* has a high growth rate and a short lifespan. Consequently, our assumptions coincide with those of Garcia Cabrera (1968) and Allue *et al.* (1977).

The estimated growth also shows that females undergo their first sexual maturation at around 5-6 months, assuming that their growth is the same as that of the males, at least until sexual maturity, and that the large cuttlefish which are inaccessible to the fishery from June to November are almost all in their second year of life.

6. CONCLUSION

From the study of cuttlefish distribution, reproduction and growth, we can draw an idea of the biological cycle of this mollusc on the Senegalese coasts.

One-year old mature, large cuttlefish reach the coast, especially at Cape Vert, from deeper grounds (90-100 m) in January (cold season). They are followed by smaller individuals under one year of age whose sexual maturation is less advanced.

The large cuttlefish swim along the coast down to Sangomar, breeding as they go. They spawn under the stimulating effect of light, especially in February-March, particularly on grassy bottoms, meadows of algae and various kinds of detritus serving as spawn supports, located off Joal and Sangomar. Some specimens which are exhausted by reproduction die. Others return to deeper waters further north from May to September (transitional and warm season) to find their preferred conditions (cold water, sandy to muddy-sandy grounds). They also find the darkness they need for their sexual maturation on these grounds.

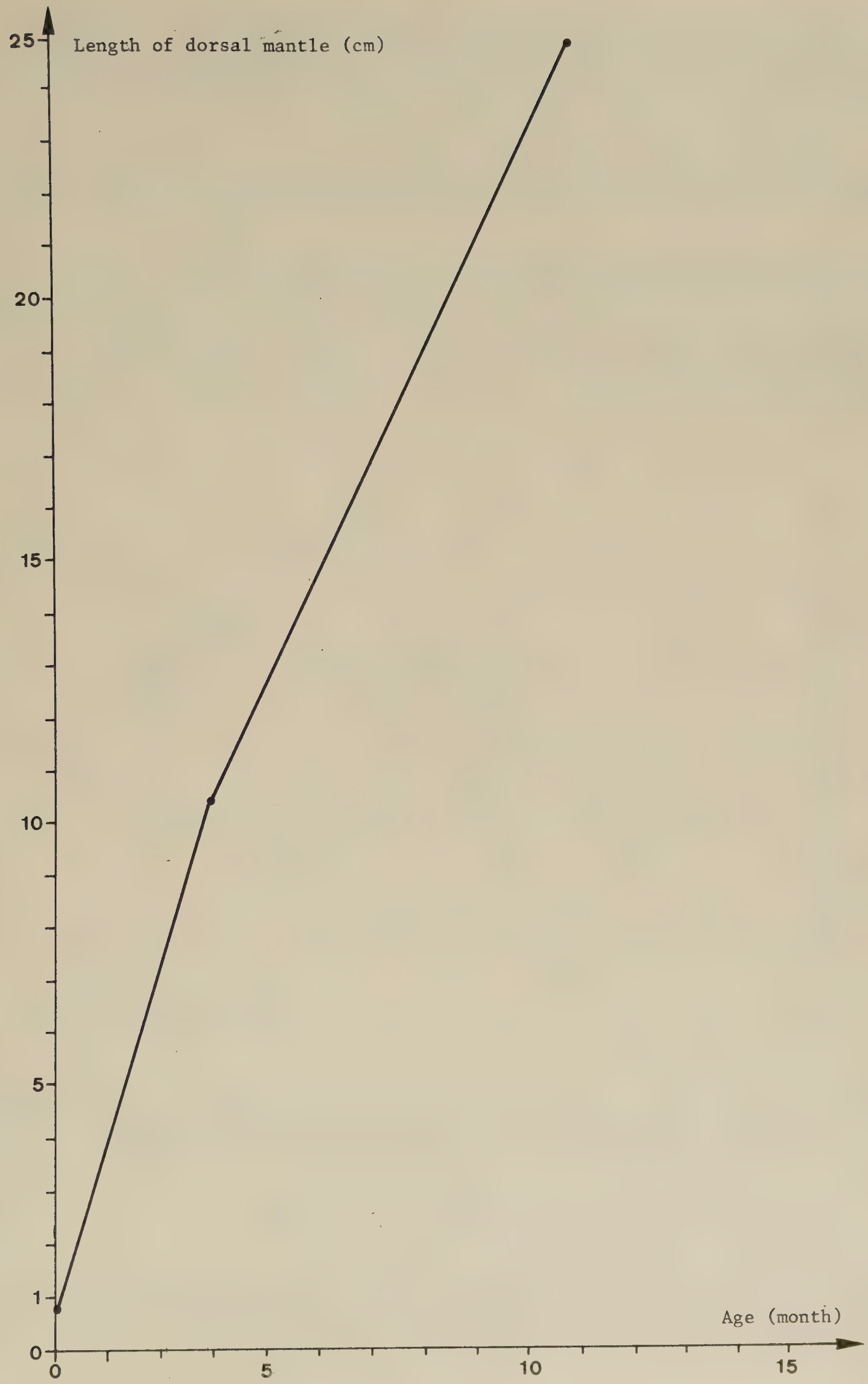


Figure 44 Male cuttlefish growth curve up to 25 cm length of dorsal mantle

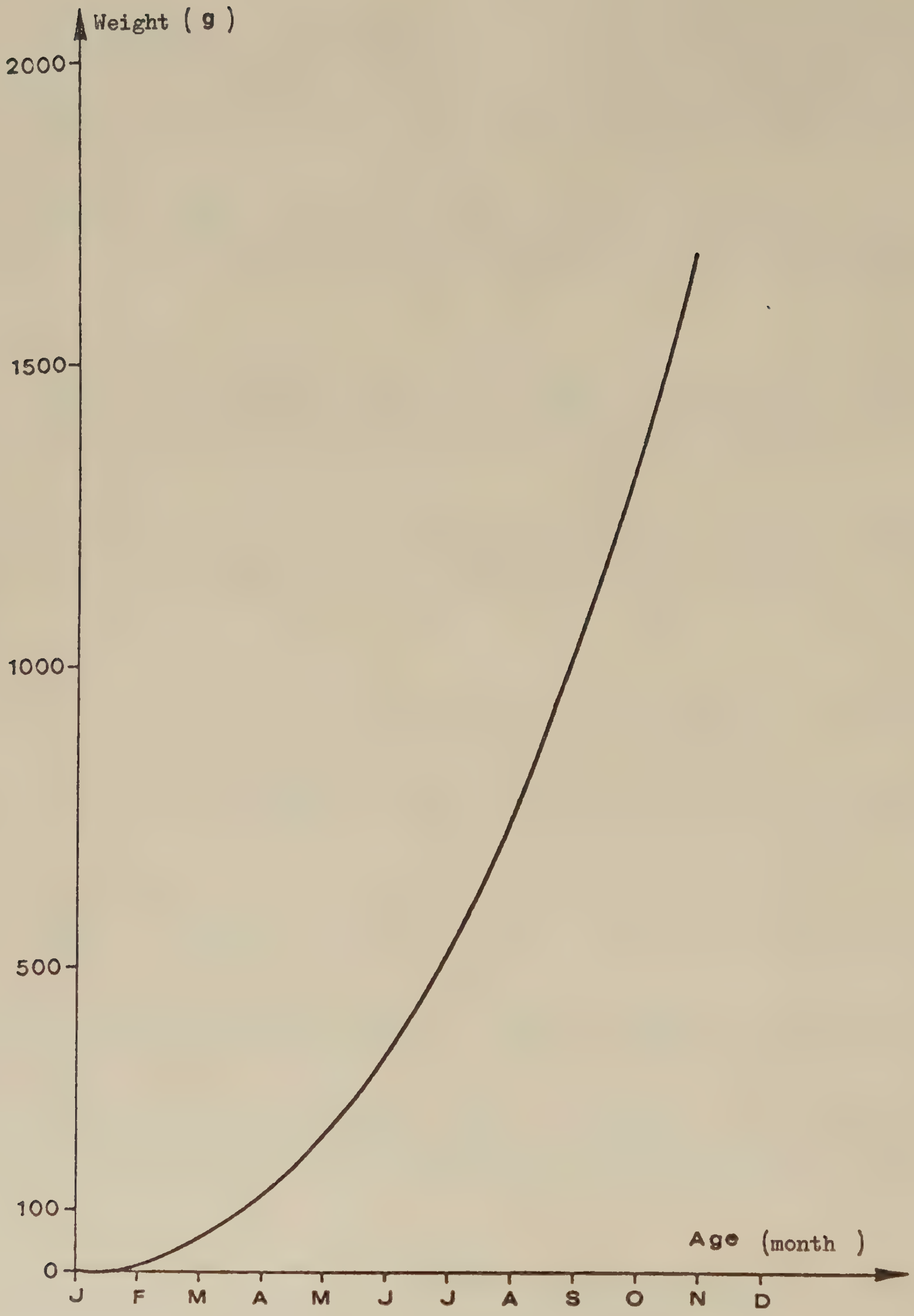


Figure 45 Male cuttlefish growth in weight

The cuttlefish under one year of age which follow those over a year old start to reach maturity in March and spawn from April to June. Some of them follow the old individuals to deep waters and return with them the following year when they are over one year old. Others possibly go down to Casamance.

It seems that another group of one-year olds comes from Guinea Bissau and goes up as far as Casamance and perhaps even further north to spawn from March to June (cold season and beginning of warm season) before returning to the south moving inshore. It has not yet been determined whether this group is part of one and the same stock as the preceding one.

Another cuttlefish group aged approximately six months appears offshore from M'Bour and Pointe Sarène in July (warm season), then migrates inshore to breed in August-September. We do not know exactly what becomes of it.

Assuming that the growth of young animals is rapid in the cold season and during the transition periods (since food is abundant inshore) and slower in the warm season (because of the scarcity of food in the environment), we believe that the third cuttlefish group which arrives inshore in July comes from the large spawn in February-March (since juveniles will have migrated to deep waters after hatching). On the other hand, the cuttlefish hatched April-June and August-September are the young individuals which accompany the large ones inshore in January and which had migrated to deep waters immediately after being born. Figure 46 gives a schematic view of the cycle.

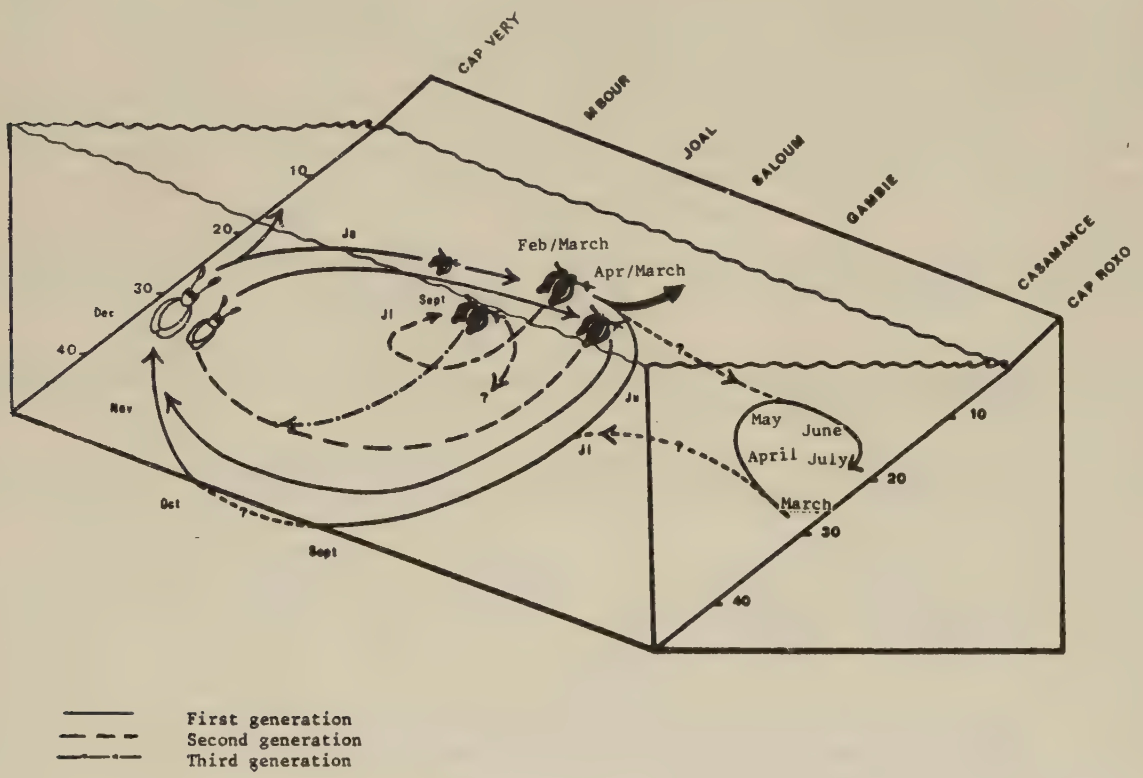

CAP VERY
M'BOUR
JOAL
SALOUM
GAMBIE
CASAMANCE
CAP ROXO
10
20
30
40
Dec
Nov
Oct
Sept
Jn
Jl
Sept
Jl
Feb/March
Apr/March
?
?
Jn
Jl
?
May
June
April
July
March
10
20
30
40
?
First generation
Second generation
Third generation

Figure 46 Hypothetical pattern of the biological cycle of the cuttlefish on the south coast of Senegambia

7. REFERENCES

Adam, W., 1941 *Cephalopoda*. Mem.Mus.R.Hist.Nat.Belg.(2), 21:83-162

__________, 1952 Expéditions océanographiques belges dans les eaux côtières africaines de l'Atlantique sud (1948-1949). Resultats scientifiques. Céphalopodes. Résult.Sci.Exped.Océanogr.Belge (1948-49), 3(3):142 p.

__________, 1960 Les céphalopodes de l'Institut Français d'Afrique Noire. 2. Bull.Inst.Fr. Afr.Noire, 22(2):465-511

Allue, C., *et al.*, 1977 Fichas de identificacion de especies. Atlantico oriental. Estrecho de Gibraltar - Cabo Verde (Zona CECAF 34). 2. Cl. Cephalopoda. Datos Inf. Inst.Invest.Pesq.,Barc., (3)

Bagenal, T.B., 1973 Fish fecundity and its relation with stock and recruitment. Rapp. P.-V. Réun CIEM, 164:186-98

Bas, C., E. Morales and J.S. Feliu, 1971 Pesquerias de cefalopodos en el Banco Sahariano. Publ.Tech.Dir.Gen.Pesca Marit.Madr., 9:129-51

Berrit, G.R., 1962 Contribution à la connaissance des variations saisonnières dans le golfe de Guinée. Observations de surface le long des lignes de navigation: etude régionale. Cah.Océanogr., 14 (9):633-43, (10):719-29

Bertalanffy, L. von, 1938 Quantitative theory of organic growth. Hum.Biol., 10(2):180-213

Bodard, M., 1968 Les *Hypnea* au Sénégal. Bull.Inst.Fondam.Afr.Noire (A Sci.Nat.), 30(3):811-25

Bodard, M. and J. Mollion, 1974 La végétation infralittorale de la Petite Côte sénégalaise. Bull.Soc.Phycol.Fr., (19)

Boely, T., 1979 Biologie de deux espèces de sardinelles des côtes sénégalaises. Thèse doctorate: Science naturelle. Université Pierre et Marie Curie, Museum National d'histoire naturelle, Paris

Boletzky, S. von, 1974 Elevage de céphalopodes en aquarium. Vie Milieu, 24,2 (A)

Boletzky, S. von, *et al.*, 1971 Laboratory rearing of Sepiolinae. Mar.Biol., 8(1):82-6

Briantais, A., 1974 Le point sur l'exploitation des céphalopodes. Pêche Marit., (1150):10-21, (1151):78-81, (1152):165-9

Cadenat, J., 1948 Bateaux et engins de pêche. In C.R.Conférence de la Pêche Maritime (Dakar, 15-22 janvier 1948)

Choe, S., 1963 Daily age markings on the shell of cuttlefishes. Nature, Lond., 197(4864): 306-7

Clarke, M.R., 1962 The identification of cephalopod "beaks" and relationship between beak size and total body weight. Bull.Brit.Mus.(Nat.Hist.)Zool., 8(10)

__________, 1965 Growth rings in the beaks of the squid *Moroteuthis ingens*. Malacologia, 3(2)

Cushing, D.H., 1975 Marine ecology and fisheries. Cambridge, Cambridge University Press, 278 p.

Dangeard, P., Algues de la presqu'île du Cap-Vert (Dakar) et de ses environs. Botaniste,
1952 36(1-4)

Domain, F., Les fonds de pêche du plateau continental ouest africain entre 17°N et 12°N.
1976 Doc.Sci.Provis.Cent.Rech.Oceanogr.Dakar, (61)

FAO, Yearbook of fishery statistics. Annuaire statistique des pêches. Anuario estadistico
1978 de pesca. Catches and landings. Captures et quantités débarquées. Capturas y desembarques. 1977. Yearb.Fish.Stat./Annu.Stat.Pêches/Anu.Estad.Pesca, (44):343 p.

Fischer, P.H., Vie et moeurs des mollusques. Paris, Payot, 312 p.
1950

Fishery Committee for the Eastern Central Atlantic (CECAF), Report of the *Ad hoc* Working
1979 Party on the assessment of cephalopod stocks. CECAF/ECAF Ser., (78/11):149 p. Issued also in French

Fontana, A., Etude de la maturité sexuelle des sardinelles de la région de Pointe Noire.
1969 Cah.ORSTOM (Hydrobiol.), 7(2):101-14

__________, Etude du stock démersal côtier congolais. Biologie et dynamique des princi-
1979 pales espèces exploitées. Proposition d'aménagement de la pêcherie. Thèse doctorat d'Etat es-science, Université Pierre et Marie Curie, Paris

Garcia Cabrera, C., Biologia y pesca del pulpo y choco en aguas del Sahara español.
1968 Publ.Tech.Junta Estud.Pesca, Madr., 7:141-98

Griffin, W.L., J.P. Warren and W.E. Grant, A bio-economic model for fish stock manage-
1979 ment. The cephalopod fishery of N.W. Africa. Rep.CECAF/TECH, Dakar, (79/16): 42 p. Issued also in French

Grimpe, G., Teuthologishe Mitteilungen. 7. Systematische Ueberscht der Nord-
1922 Seecephalopoden. Zool.Anz., 52

Gheno, Y. and J.C. Le Guen, Détermination de l'âge et croissance de *Sardinella eba* dans
1968 la région de Pointe Noire. Cah.ORSTOM (Océanogr.), 6(2):69-82

Guerra, A., Determinación de la differentes fases del desarollo sexual de *Octopus*
1975 *vulgaris* mediante un indice de madurez. Invest.Pesq.,Bar., 39(2):397-416

__________, Distribución y abundancia de *Octopus vulgaris* en el Atlantico centro
1979 oriental (26°10'N-23°30'N). CECAF/ECAF Ser., (78/11):83-97

Hatanaka, H., Geographical distribution of two subspecies of *Sepia officinalis* L. off
1979 the northwestern coast of Africa. CECAF/ECAF Ser., (78/11):55-62

Hotta, M., Production, trade and consumption of Cephalopods and Cephalopod products.
1976 FAO Fish.Circ., (340):83 p.

ISRA/ORSTOM, La reproduction des espèces exploitées dans le Golfe de Guinée. Dakar,
1979 9-12 novembre 1977. Doc.Sci.Cent.Rech.Océanogr.,Dakar-Thiaroye, (68):213 p.

Ikeda, I., *et al.*, Observations on *Sepia* egg clusters caught during commercial trawling
1976 operations in the CECAF area. FAO Fish.Rep., (183):65-71

Kristensen, J., The coastal waters of the Netherlands as an environment of molluscan life.
1959 Basteria, Tydsch.Ned.Malacol.Ver., 23 Suppl.

Le Guen, J.C., Dynamique des populations de *Pseudobthus (Fonticulus) elongatys* (Bowd.
1971 1825). Poissons - Sciaenidae. Cah.ORSTOM (Océanogr.), 9(1):2-84

Lipinski, M., A preliminary study on ageing of squids from the statoliths. Special meeting of scientific council, February 1980. NAFO/SCR Doc. 80/II/12
1980

Mangold, K., Biologie des Céphalopodes benthiques et nectoniques de la mer Catalane. Vie Milieu, Suppl.13:259 p.
1963

__________, *Sepia officinalis* de la mer Catalane. Vie Milieu (A Biol.Mar.), 17(2): 961-1012
1966

Mangold, K. and R. Boucher Rodoni, Rôle du jeûne dans l'induction de la maturation génitale chez les femelles d'*Eledone cirrosa*. C.R.Hebd.Séances Acad.Sci.,Paris (D), 276
1973

Mangold, K. and P. Fioroni, Morphologie et biométrie des mandibules de quelques Céphalopodes méditerranéens. Vie Milieu (A Biol.Mar.), 17(3):1139-96
1966

Mangold, K. and D. Froesch, A reconsideration of factors associated with sexual maturation. Symp.Zool.Soc.Lond., 38:541-55
1977

Mangold, K., *et al.*, Factors affecting sexual maturation in Cephalopods. Publ.Stn.Zool. Napoli, 39 Suppl.:259-66
1975

Mesnil, B., L'exploitation des Céphalopodes, situation et perspectives. Sci.Pêche, (265):21 p.
1977

Mollion, J., Etude préliminaire des *Hypnea* au Sénégal comme source de phycocolloides. Bot.Mar., 16(4):221-5
1973

__________, Etude quantitative d'une formation végétale marine de l'infralittoral supérieur au Sénégal. Bull.Inst.Fondam.Afr.Noire (A Sci.Nat.), 37(3):
1975

Morales, E. and A. Guerra, Céphalopodes du N.W. de l'Afrique. CIEM. CM. 1975/K8 Comité des crustacés, coquillages et benthos (mimeo)
1975

Naef, A., Ueber neue Sepioloden aux me von Neapel. Publ.staz.Zool.Napoli:I
1961

Rang, S., Documents pour servir à l'histoire naturelle des Céphalopodes cryptodibranches. Mag.Zool.:VII
1837

Richard, A., La température facteur externe de la croissance pour le céphalopode *Sepia officinalis* L. C.R.Hebd.Séances Acad.Sci.,Paris (D), 263(16):1138-41
1966

__________, Rôle de la photopériode dans le déterminisme de la maturation génitale femelle du céphalopode *S. officinalis* L. C.R.Hebd.Séances Acad.Sci.,Paris (D), 264(10):1315-8
1967

__________, Mise en évidence de l'action de la lumière dans le déterminisme de la ponte chez le céphalopode *Sepia officinalis* L. C.R.Hebd.Séances Acad.Sci.,Paris (D), 267(26):2360-3
1968

__________, The part played by temperature in the rhythm of formation of markings on the shell of cuttlefish (*S. officinalis*). BIRKNAUSER Verlag, Basel, Schewiz. Separatum experientia 25
1969

__________, Analyse du cycle sexuel chez les céphalopodes: mise en évidence expérimentale d'un rythme conditionné par les variations de facteurs externes et internes. Bull.Soc.Zool.Fr., 95
1970

__________, Action qualitative de la lumière dans le déterminisme du cycle sexuel chez le céphalopode *Sepia officinalis* L. C.R.Hebd.Séances Acad.Sci.,Paris (D), 272(1):106-9
1971

Richard, A., La coquille de *Sepia officinalis*, stries et interstries, leurs variations
1972 en rapport avec l'écologie de l'animal. Haliotis, 2(2)

____________, Rythmes sexuels chez les céphalopodes, étude expérimentale du cycle bio-
1972a logique de la seiche. *S. officinalis.* Haliotis, 2(1)

Richard A. and J. Lemaire, Déterminisme et différenciation sexuelle chez la seiche
1975 *Sepia officinalis* L. Pubbl.Stn.Zool.Napoli, 39 Suppl.

Rochebrune, A.T., Merveilles de la nature. Les vers, les mollusques, les échinodermes,
1884 les zoophytes, les protozoaires et les animaux de grandes profondeurs. Paris,
J.B. Baillière et Fils

Rowe, V.L. and K. Mangold, The effect of starvation on sexual maturation in *Illex*
1975 *illecebrosus.* J.Exp.Mar.Biol.Ecol., 17(2):157-64

Teissier, G., La relation d'allométrie; sa signification statistique et biologique.
1948 Biometrics, 4(1)

Tinbergen, L., Zur fortpflanzungsethologie von *Sepia officinalis* L. Arch.Neerl.Zool., 3
1939

Touré, D., Variations quantitatives et qualitatives du zooplancton dans la région du
1972 Cap-Vert de septembre 1970 à août 1971. Doc.Sci.Provis.Cent.Rech.Océanogr.,
Dakar, (39)

Voss, G.L., Cephalopod resources of the world. FAO Fish.Circ., (149):79 p.
1973

Wells, M.J. and J. Wells, Hormonal control of sexual maturity in *Octopus.* J.Exp.Biol.,
1959 36(1):1-33

____________, Pituatary analogue in the *Octopus.* Nature, Lond., 222(5190):293-4
1969

____________, Optic glands and the state of the testis in *Octopus.* Mar.Behav.Physiol., 1
1972

Worms, J., Introduction à l'étude des populations de céphalopodes de la Méditerranée
1977 occidentale avec référence particulière à l'encornet *L. vulgaris.* D.E.A.,
Université des Sciences et Techniques du Languedoc, Montpellier

____________, Biologie et pêche des céphalopodes. 2. La pêche en Méditerranée, évolu-
1979 tion et perspective. Pêche Marit., (1212)

____________, L'utilisation des prises commerciales en biologie des pêches. Application
1979a à l'étude d'une population de *L. vulgaris* du golfe du Lion. Thèse 3ème cycle,
Université des Sciences et Techniques du Languedoc, Montpellier

Yamamota, T. and M. Ansa-Emmim, CECAF project statistical survey. Las Palmas based
1979 international trawlers, February 1978-February 1979. Rep.CECAF/TECH, Dakar,
(79/15):15 p.

Yoshinobu, Y., K. Takeshi and N. Masahara, Biological studies of squids and cuttlefish
1971 stocks. 3. On the growth patterns of the shell of *Sepia officinalis*,
cuttlefish trawled in the western coastal sea of Africa. Bull.Tokai Reg.Fish.
Res.Lab., (66)

CEPHALOPOD RESOURCES IN THE INDO-PACIFIC REGION[1/]

by

S. Chikuni
Fisheries Department
FAO, Rome

ABSTRACT

In view of the rapidly increasing importance of the exploitation of cephalopod resources for all the nations in the Indo-Pacific region, the information available on the resources and the fisheries has been reviewed.

Two productive areas in the region - the waters around Japan and further north, and around New Zealand - where intensive large-scale commercial fishing directed specifically for cephalopods has been currently carried out, are excluded from this review as the results of the study on those resources have already been fairly well documented by a number of publications. In this study the remaining areas have been divided into seven sub-areas as the nature of the resources and the state of exploitation on them differ greatly by localities, namely, (1) Yellow Sea and East China Sea, (2) waters around the Philippines, (3) South China Sea, (4) Java Sea to northern Arafura Sea, (5) waters around Australia, (6) Bay of Bengal and (7) Eastern Arabian Sea.

The information and the data available are still very poor and fragmentary in the region. However, an overall view on the major resources of neritic cephalopods (cuttlefish, neritic squid and octopus) available in each of the areas has been obtained. The commercial fishing currently directed toward cephalopods in each area has generally been small in comparison to the vast extent of the possible fishing grounds (both horizontally and vertically) and supposedly large potential yields there. This is especially true for the local fisheries in the Indonesian and Australian waters. The resources in the waters around the Philippines, the Bay of Bengal and the Eastern Arabian Sea appear also to have been only slightly exploited, but the potential yield to be expected in these areas may be smaller than those in the other areas. The Yellow Sea, East China Sea and the South China Sea, where some local stocks have been intensively fished, still seem to offer opportunities for further expansion of the exploitation of several resources.

It is noticeable in many countries that the bulk of the catch of neritic cephalopods is taken by the larger trawlers. The pelagic stages of cuttlefish and neritic squid, specifically the latter, have been utilized in only a few localities, which suggests the value of introducing suitable fishing methods to the small-scale fisheries in the region. The same applies to octopus resources which are only taken in substantial numbers by trawlers in the Gulf of Thailand.

The potential yield of the neritic cephalopods has been roughly estimated to be about 1.1-1.4 million tons from the entire region compared with the current catch of about 0.3 million tons. Some problems involved in the future development of the cephalopod fishery are discussed specifically in connection with the nature of small-scale fisheries in the region. Recommendations on the studies required in the immediate future have also been made.

Few but positive indications on harvesting several oceanic squids have been obtained. However, the information collected so far does not appear to be sufficient to assess the stocks for the immediate commencement of commercial fishing on them. Further surveys and studies on both biology and environment are required.

Special attention should be given to the regional and interregional collaboration for surveys and studies of cephalopods resources (both neritic and oceanic) as many resources occur over the two or more areas of national jurisdiction.

[1/] Excluding the waters around New Zealand, Papua New Guinea, Korean Peninsula, Japan and further north

RESUME

Etant donné l'importance de plus en plus grande que prend l'exploitation des ressources de céphalopodes dans tous les pays de la région Indo-Pacifique, on a réexaminé l'information disponible sur ces ressources et sur leur pêcherie.

Cet examen n'a pas pris en considération deux zones productives de la région - les eaux situées aux alentours du Japon et celles qui sont situées plus au nord et aux alentours de la Nouvelle-Zélande - où l'on pratique couramment une pêche commerciale intensive et de grande ampleur essentiellement de céphalopodes, car ces zones avaient déjà fait l'objet d'une étude approfondie dont les résultats figurent dans plusieurs ouvrages. Les autres zones, examinées dans la présente étude, ont été divisées en sept régions subsidiaires car la nature des ressources et leur stade d'exploitation diffèrent beaucoup d'un emplacement à l'autre, à savoir (1) mer Jaune et mer de Chine orientale, (2) eaux aux alentours des Philippines, (3) mer de Chine méridionale, (4) de la mer de Java à la mer septentrionale d'Arafura, (5) eaux aux alentours de l'Australie, (6) golfe du Bengale et (7) mer d'Arabie septentrionale.

On n'a pu obtenir que quelques renseignements et données très fragmentaires sur la région. Cela a cependant permis d'avoir une vue d'ensemble sur les principales ressources de céphalopodes néritiques (seiches, encornets néritiques et poulpes). La pêche commerciale des céphalopodes qui est pratiquée actuellement dans chacune de ces régions est peu importante par rapport aux vastes fonds de pêche à exploiter (aussi bien horizontalement que verticalement) et au rendement potentiel élevé. Cela est particulièrement vrai pour les pêcheries locales dans les eaux indonésiennes et australiennes. Les ressources dans les eaux aux alentours des Philippines, dans le golfe du Bengale et dans la mer d'Arabie septentrionale semblent aussi n'avoir été que peu exploitées mais dans ces zones le potentiel pourrait être plus faible que dans les autres zones. Dans la mer Jaune, la mer de Chine septentrionale et la mer de Chine méridionale où certains stocks locaux ont été intensivement pêchés, il semble cependant qu'il soit encore possible d'accroître l'exploitation de plusieurs stocks. On peut remarquer dans plusieurs pays que le gros des prises de céphalopodes néritiques est capturé par de grands chalutiers. Les stades pélagiques des seiches et des encornets néritiques, particulièrement de ces derniers, n'ont été utilisés que dans quelques emplacements, ce qui laisse à penser qu'il serait très utile d'introduire des méthodes de pêche appropriées dans les pêcheries artisanales de la région. Il en est de même des poulpes qui ne sont capturés en grand nombre que par des chalutiers dans le golfe de Thaïlande. Le rendement potentiel des céphalopodes néritiques a été estimé à environ 1,1 -1,4 million de tonnes dans l'ensemble de la région alors que les captures ne représentent actuellement qu'environ 0,3 million de tonnes. On examine certains problèmes que pose le développement futur des pêcheries de céphalopodes, problèmes qui tiennent à la nature des pêcheries artisanales de la région. On a également formulé des recommandations sur les études à entreprendre dans un proche avenir.

On a obtenu quelques renseignements positifs sur l'exploitation de plusieurs encornets océaniques mais il semble qu'ils ne soient pas assez complets pour que l'on puisse évaluer des stocks en vue de commencer immédiatement à les exploiter sur une base commerciale. Il faut entreprendre d'autres enquêtes et études aussi bien sur la biologie que sur le milieu.

Il faudrait accorder une attention spéciale à la collaboration régionale et interrégionale pour ces enquêtes et ces études sur les ressources de céphalopodes (aussi bien néritiques qu'océaniques) car bon nombre d'entre elles se trouvent dans deux ou plusieurs zones de juridiction nationale.

RESUMEN

Dado que la explotación de los cefalópodos va adquiriendo cada vez más importancia en todos los países de la región del Indo-Pacífico, se ha revisado la información existente sobre recursos y pesquerías.

Quedan excluidas de este examen dos zonas productivas de la región (las aguas en torno al Japón y hacia el norte, y las que circundan Nueva Zelandia), donde existe ya una pesquería comercial intensiva y a gran escala concentrada específicamente en los cefalópodos, porque los resultados del estudio de esos recursos ya están bien documentados en toda una serie de publicaciones. En el presente estudio, las zonas restantes se han dividido en siete subzonas, ya que la índole de los recursos y el estado de su explotación difiere mucho según los lugares, a saber: (1) mar Amarillo y mar de China oriental, (2) aguas en torno a Filipinas, (3) mar de China meridional, (4) mar de Java hasta la parte septentrional del mar de Arafura, (5) aguas en torno a Australia, (6) bahía de Bengala y (7) mar Arábigo oriental.

La información y los datos disponibles en la región son aún muy deficientes y fragmentarios. Sin embargo, se ha conseguido una visión general de los principales recursos de cefalópodos neríticos (jibias, calamares neríticos y pulpos) existentes en cada una de las zonas. La pesquería comercial de cefalópodos en cada una de esas zonas ha sido generalmente pequeña, en comparación con la gran cantidad de caladeros posibles (tanto horizontal como verticalmente) y el gran rendimiento potencial que se supone existe, lo cual es especialmente cierto para la pesquería local en aguas de Indonesia y de Australia. Parece que también se han explotado muy poco los recursos de las aguas en torno a Filipinas, la bahía de Bengala y el mar Arábigo oriental, pero el rendimiento que puede esperarse de estas zonas es menor que el de los otras. El mar Amarillo-mar de China oriental y el mar de China meridional, donde se han pescado intensamente algunas poblaciones locales, parecen ofrecer aún oportunidades para aumentar la explotación de varios recursos. En muchos países, la mayoría de las capturas de cefalópodos neríticos las hacen los grandes arrastreros. Las fases pelágicas de la jibia y de los calamares neríticos, concretamente de los últimos, no se han utilizado sino en pocas localidades, lo cual sugiere la importancia de introducir métodos idóneos de pesca para las pequeñas pesquerías de la región. Lo mismo vale para los recursos de pulpos, explotados sólo en cantidad considerable por arrastreros en el golfo de Tailandia.

El rendimiento potencial de los cefalópodos neríticos se ha estimado en torno a 1,1-1,4 millones de toneladas en toda la región, frente a una captura actual de unos 0,3 millones de toneladas. Se examinan algunos problemas que plantea el desarrollo futuro de la pesquería de cefalópodos, atendiendo sobre todo a las pequeñas pesquerías de la región, y se hacen recomendaciones sobre los estudios que hacen falta en el futuro inmediato.

Las indicaciones conseguidas sobre la captura de varios calamares oceánicos son pocas, pero positivas. Sin embargo, no son suficientes para evaluar las poblaciones, con vistas a iniciar inmediatamente une pesquería comercial. Hacen falta más reconocimientos y estudios biológicos y del medio.

Deberá prestarse especial atención a la colaboración regional e interregional en los reconocimientos y estudios de los recursos de cefalópodos (neríticos y oceánicos), ya que muchos recursos se hallan en dos o más zonas de jurisdicción nacional.

1. INTRODUCTION

It is well known that in cephalopod production the Indo-Pacific region is high and the catches account for about 70-75 percent of the total world catch (Table 1). However, the majority of the catch has been mostly taken from a few limited waters in the region, around Japan since the early 20th Century (FAO 1976, Okutani 1977) and more recently around New Zealand where distant fishing fleets from Japan, the USSR and the Republic of Korea have been intensively exploiting squids (Smith, Roberts and Hurst 1981 and Mattlin 1982). The total catch in these two areas accounts for about 70-75 percent of the total catch from the entire region. In contrast, the catch from the rest of the region, south of Japan and west of New Zealand, has still remained at a low level in spite of the vast extent of the areas and the supposedly large potential yield there (Table 1).

Table 1

Nominal catch of cephalopods by area in the Indo-Pacific region in 1970 and 1975-81[a/]
('000 t)

Area	1970	1975	1976	1977	1978	1979	1980	1981
I Currently Productive Areas								
Northern Northwest Pacific[b/]	609	603	575	531	567	593	750	603
Waters around New Zealand	-	20	20	55	36	49	79	60
(Sub-Total)	(609)	(623)	(595)	(586)	(603)	(642)	(829)	(663)
II Remaining Areas[c/]								
Yellow Sea and East China Sea	78	62	81	79	103	145	131	81
Waters around the Philippines	18	32	26	27	32	29	32	32
South China Sea	48	87	92	113	118	102	94	91
Java Sea to northern Arafura Sea	8	11	10	10	10	14	13	13
Waters around Australia	0	9	8	3	6	17	12	12
Bay of Bengal	1	4	3	11	10	12	9	9
Eastern Arabian Sea	0	5	6	8	19	15	12	14
(Sub-Total)	(153)	(210)	(226)	(251)	(298)	(334)	(303)	(252)
Region Total	762	833	821	837	901	976	1 132	915
World Total[d/]	999	1 183	1 211	1 231	1 330	1 522	1 530	1 304

[a/] Source: FAO Statistical Yearbooks, Silas *et al.* (1982), and Taiwanese Statistics on demersal fish

[b/] Waters around Korean peninsula, Japan and further north

[c/] See text for the details on the definition of the areas; see also Tables 4-10 for details and problems involved in the statistics

[d/] Catch by Taiwanese long-range trawl fleet is not included

The bulk of the catches from the above-mentioned two productive waters is limited to a few species of squids, *Todarodes pacificus*, *Ommastrephes bartrami* and *Onychoteuthis borealijaponica* for the former waters and *Nototodarus sloani* and probably *N. gouldi* (see Section 2.2.1) for the latter. Surveys and studies on these resources have been carried out by a number of institutes/scientists and are well documented in many publications including the fishing gear and methods employed in the commercial fisheries, e.g., FAO 1976, Okutani 1977, Ishii 1977, Murata, Ishii and Araya 1976, Murata and Ishii 1977, Murata and Shimazu 1982, and Tung 1981 for the first, and FAO 1976, Kawakami 1976, Kawakami and Okutani 1981, Okutani 1977, Roberts 1978, Tung 1978, Smith, Roberts and Hurst 1981 and Mattlin 1982 for the second. It appears that the stocks of *T. pacificus* around Japan have been fully exploited and those of *O. bartrami* and *O. borealijaponica* along the northern Pacific coast of Japan to the Kuril Islands have been nearly fully exploited. The state of the exploitation of *N. sloani* and *N. gouldi* around New Zealand is not known, however, some stocks may have been fairly heavily fished with the current annual catches of about 50-80 000 t. The other cephalopod resources around Japan, including cuttlefish and squid and their utilization in Japan have been well reviewed by Yoshikawa (1978) and most of the stocks appear to have been fully exploited.

With the exception of a few local stocks in the Gulf of Thailand, the Yellow Sea-East China Sea and the waters around Hong Kong, cephalopod resources in the remaining areas have not been intensively exploited in spite of the fact that all the nations in the area have traditionally accepted cephalopods as food. Australia is an exception, but this is now changing. However, many of those nations, including Australia, have recently started plans to intensify the exploitation of cephalopods in their new areas of extended jurisdiction aiming firstly to earn foreign exchange by exporting cephalopod products and secondly to increase the domestic supply of animal protein (Hotta 1982, a). Thailand has made great strides in exporting cephalopod products during the past decade, and more recently India, Malaysia and the Philippines started active exportation of cephalopod products, while the increase in the domestic consumption is noteworthy, particularly in Indonesia and the Philippines. As the results of these trends on cephalopod demands, while the catches in the northern Northwest Pacific and in the waters around New Zealand have remained stable (Table 1), the catches in each of the remaining areas shows a steady increase during the past decade.

In these circumstances, the Standing Committee on Resources Research and Development (SCORRAD) of the Indo-Pacific Fishery Commission (IPFC) focused its attention on the importance of the development of cephalopod fisheries and the rational utilization of the resources in the Indo-Pacific region at its Third Session in Sydney, Australia during 28 April - 4 May 1982 (IPFC 1982). The meeting clarified several important lines to be taken into account for the future development of the fishery and resources management.

Biological information on cephalopod resources in the Indo-Pacific region is very sparse with the exception of the waters around Japan and New Zealand and the technical know-how on catching cephalopods is generally very poor. These two facts interact and support each other. In fact, most of the current catch is being taken by coastal trawlers as a by-catch, except for few very localized aimed fishing in China, Hong Kong, Indonesia and Malaysia, of which the data are too fragmentary to evaluate the distribution and potential of those resources in the entire region.

The two better known waters, the northern Northwest Pacific and the waters around New Zealand, are excluded from review in this paper. The waters around the Papua New Guinea and the southwestern Pacific Islands are also excluded where almost no information on cephalopods is available.

The sub-areas referred to in this paper (Figure 1) are defined as:

(a) Yellow Sea and East China Sea: including the northwestern South China Sea along the coasts of China, Taiwan, Province of China and Hong Kong;

(b) waters around the Philippines;

(c) South China Sea: including the Gulf of Thailand and Malacca Strait but excluding the northwestern part of the South China Sea as mentioned above;

(d) Java Sea to northern Arafura Sea: including the Indian Ocean along the Indonesian coast;

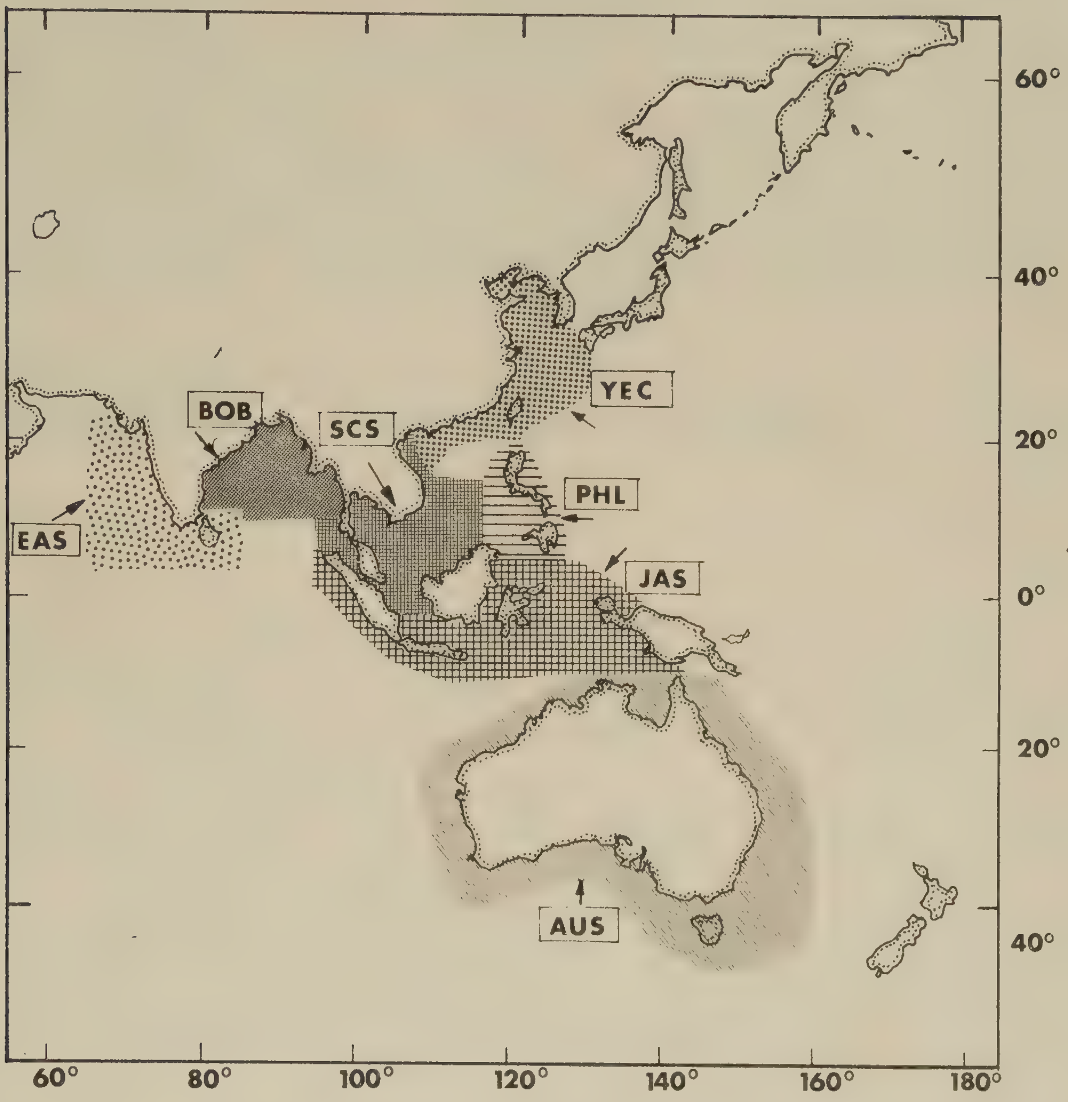

YEC
PHL
SCS
JAS
AUS
BOB
EAS
60°
40°
20°
0°
20°
40°
60°
80°
100°
120°
140°
160°
180°

Figure 1 Sub-areas defined in the study

YEC: Yellow Sea and East China Sea
PHL: waters around Philippines
SCS: South China Sea
JAS: Java Sea to Northern Arafura Sea
AUS: waters around Australia
BOB: Bay of Bengal
EAS: Eastern Arabian Sea

(e) waters around Australia;

(f) Bay of Bengal: including the Andaman Sea; and

(g) Eastern Arabian Sea: including the waters around Sri Lanka and the west coast of India, and the Loccadive Islands.

The selection of these areas has been made taking into account firstly the geographic location and oceanographic/climatic conditions of the waters and secondly the state and the similarity of existing fishery along the coasts. The areas represent, as a result, reasonably the single or combined national EEZs of the countries concerned. It should also be noted that the two marginal waters in the north and south, namely from the Yellow Sea to the northern East China Sea and the waters along the southeast to southwest coast of Australia are somewhat different in climatic and oceanographic conditions from the vast central part of the region where the tropical climate and monsoon regime rule the environment. The defined areas seem, therefore, to accord reasonably well with the ecological difference of cephalopods inhabiting the entire region.

Cephalopod species have been grouped into four categories, namely: (1) cuttlefish, (2) neritic squid, (3) oceanic squid and (4) octopus - see the following section for the details so as to discuss the feature of these resources more clearly from the biological/ecological point of view.

2. MAJOR RESOURCES IN THE REGION

2.1 Species

No comprehensive review has been made so far of the species occurring in the region. FAO plans to publish an annotated catalogue of cephalopod species in the world in the FAO Fisheries Synopsis Series in the near future, and also plans to prepare Species Identification Sheets of Cephalopods for the eastern Indian Ocean and western Central Pacific. However, this material is not available to be incorporated in this paper.

Voss (1973) made a global review of cephalopod resources in the world but the descriptions were incomplete for this particular region in terms of the species involved and their distribution due to lack of information at the time the work was carried out. With regard to the commercially important cuttlefish and squid resources, Okutani (1980) summarized the updated information on a worldwide basis for 86 species which cover the major species occurring in the Indo-Pacific region fairly well, however, the descriptions of their geographic distribution for several species are incomplete. Cephalopods in the waters around Hong Kong (Voss and Williamson 1971) and the Philippines (Voss 1963) are also fairly well documented, but appear to be incomplete for the same reason mentioned above. Catalogues prepared by Silas (1968) for cephalopods in the Indian Ocean and by Perera (1975) for the waters around Sri Lanka also appear to be incomplete in terms of the coverage of species and their geographic distribution, although the catalogues are useful to check the major important species in the western part of the region. Tung (1978a) reviewed the species of cuttlefish and squid occurring in the waters around Taiwan, Province of China. Dong (1981) and Dong *et al.*, (1981) also reviewed the major species occurring along the Chinese coast from information on fisheries and larvae respectively, which is also useful although the descriptions are rather sketchy. Cuttlefish and squid around Australia have been briefly reviewed by Dunning (1982) but this does not sufficiently cover all the major species especially cuttlefish. Information on octopus is almost non-existent; only fragmentary data is available (Aoki *et al.*, 1965, Silas 1968, Voss 1973, Davidson 1976, Anon 1980, a, 1981, Dong 1981, Dong *et al.*, 1981).

In addition to the above, by putting together all the sparse data from various sources the major species occurring in the region can be summarized as follows (extrapolations and interpolations were made by the author for the areas where no information is available).

2.1.1 Cuttlefish

Family Sepiidae

Sepia pharaonis
S. esculenta
S. recurvirostra
Sepiella japonica
S. apama
S. aculeata
S. prashadi
S. inermis
S. lycidas
S. kobiensis
S. latimanus

2.1.2 Neritic squid

Family loliginidae

Loligo edulis[1]
L. chinensis
L. singhalensis
Sepioteuthis lessoniana
L. japonica
L. uyii
L. duvaucelii
S. australis

Family Ommastrephidae

Todarodes pacificus
N. gouldi
Nototodarus philippinensis

2.1.3 Oceanic squid

Family Onychoteuthidae

Onychoteuthis banksii

Family Ommastrephidae

Todarodes filippovae
Symplectoteuthis oualaniensis
Ommastrephes bartrami

2.1.4 Octopus

Family Octopodidae

Octopus vulgaris
O. ocellatus
O. aegina
O. tetricus
O. macropus
Cystopus indicus

There may be several additional edible cephalopod species which could occasionally be taken by the fisheries in the region. However, the amount of those catches does not appear to be large, presumably less than 10 percent of the total cephalopod catch. They may include *Sepia andreana*, *S. savignyi*, *Sepiolina nipponensis*, *Loligo bleekeri*, *L. sibogae*, *Thysanoteuthis rhombus* (oceanic), and several species of Sepiolidae and Enoploteuthidae.

2.2 Biological Characteristics of Each Species

2.2.1 Distribution

Occurrence of the major species of cephalopod in each of the sub-areas in the region is summarized in Table 2. The two marginal waters in the north and south are somewhat different in climatic and oceanographic conditions from the vast central part of the region as was discussed in the previous section and, therefore, have somewhat different species.

---

[1] Two sub-species, *L. edulis edulis* and *L. edulis budo*, have been identified from the waters around Japan to the southern Chinese coast (Okutani 1980). However, the sub-species composition of the species identified as *L. edulis* in many waters in the region is not clear. In northern Australian waters two forms of this species (large and small) which mature at different sizes have been reported (Dunning 1982) which suggests that two sub-species exist there.

Table 2

Occurrence of the major species of cephalopods in each of the sub-areas in the Indo-Pacific region

Species[b]	Sub-area[a]						
	Y.- E. China Sea	Around the Philippines	South China Sea	Java - North Arafura Sea	Around Australia	Bay of Bengal	Eastern Arabian Sea
Cuttlefish							
S. pharaonis	+	++	++	+	+[N]	+	++
S. lycidas	+	++	++	(+)	(none)	none	none
S. aculeata	+	+	+	(+)	(none)	+	+
S. recurvirostra	+	++	++	+	(none)	(+)	(+)
S. latimanus	(+)	+	+	+	+[N]	+	(+)
S. esculenta	++	++	(+)	(+)	(+)[N]	(+)	(+)
S. kobiensis	+	(+)	(+)	(none)	(none)	+	+
S. apama	none	none	none	none	++[S]	none	none
S. prashadi	none	none	none	none	none	(+)	++
Sla. japonica	+++	none	none	none	none	none	none
Sla. inermis	none	none	+	(+)	(none)	+	+
Neritic squid							
L. edulis[c]	++	++	++	++	++[N]	+	+
L. chinensis	++	+	+++	++	++[N]	++	(+)
L. singhalensis	+	+	+	+	+[N]	+	+
L. duvaucelii	+	++	++	++	(+)[N]	++	++
L. japonica	+	(none)	(none)	none	none	none	none
L. uyii	+	(+)	+	(+)	(none)	(none)	none
Sep. lessoniana	+	+	++	+	+[N]	+	++
Sep. australis	none	none	none	none	+[S]	none	none
Tod. pacificus	++	(+)	none	none	none	none	none
Not. philippinensis	+	+	+	(+)	(none)	+	+
Not. gouldi	none	none	none	none	+++[S]	none	none
Oceanic squid							
Ony. banksii	(none)	+	+	+	+[NS]	+	+
Omm. bartrami	(+)	(+)	none	none	+[S]	none	none
Sym. oualaniensis	+	+	+	+	+[N]	+	+
Tod. filippovae	none	none	none	none	+[S]	none	none
Octopus							
O. vulgaris	+	+	+	+	+[N]	+	+
O. aegina	+	+	+	+	(+)[N]	+	+
O. macropus	+	+	+	+	(+)[N]	+	+
O. ocellatus	+	none	none	none	none	none	none
O. tetricus	none	none	none	none	+++[S]	none	none
Cy. indicus	+	+	+	(+)	(none)	+	+

+ : present; ++ : abundant; +++ : highly abundant; (+) : probably present; (None) : probably none

[a] See text for the definition (Introduction)

[b] *S.: Sepia; Sla.: Sepiella; L.: Loligo; Sep.: Sepioteuthis; Tod.: Todarodes; Not.: Nototodarus; Ony.: Onychoteuthis; Omm.: Ommastrephes; Sym.: Symplectoteuthis; O.: Octopus; Cy: Cystopus*

[c] See text for the problems in the species identification (footnote in Section 2)

[N] Northern Australia only

[S] Southern Australia only

The Yellow Sea to the northern East China Sea is characterized by (1) predominance of *Sepiella japonica*, (2) abundant distribution of *Sepia esculenta*, *Todarodes pacificus* and (3) presence of *Octopus ocellatus* while the waters along the southeast-southwest coast of Australia by (1) *Nototodarus gouldi* and *Octopus tetricus*, (2) *Sepia apama*, and (3) *Todarodes filippovae*. It should be noted here that the taxonomic studies recently carried out suggest that *N. gouldi* may be abundantly distributed also in the neighbouring New Zealand waters (Kawakami and Okutani 1981, Smith, Roberts and Hurst 1981) but are supposedly different stocks from those in the Australian waters. However, *N. sloani* which is a taxonomically very close species and is abundantly distributed in the New Zealand waters (Kawakami 1976, Kawakami and Okutani 1981, Smith, Roberts and Hurst, 1981, Mattlin 1982), has not been reported from the Australian waters.

With the exception of these areas many species occur widely. Among cuttlefish and neritic squid *Sepia pharaonis*, *S. latimanus*, *Loligo edulis*, *L. chinensis*, *L. singhalensis*, *L. duvaucelii* and *Sepioteuthis lessoniana* are common throughout the tropical sub-areas. It should be noted here that there is some doubt on species identification of *Loligo edulis*. Although the species appear to be abundant throughout the area, it may possibly be composed of a number of sub-species as mentioned previously. If this is the case the appraisal should be modified accordingly.

Oceanic squid can be grouped into two, (1) warm water types which are distributed in a wide belt area extended to north and south symmetrically from the tropical zone and (2) cold water types which form one or two belt(s) of habitat in temperate to cold waters. The former group includes *Onychoteuthis banksii* and *Symplectoteuthis oualaniensis* and the latter *Ommastrephes bartrami* (in both the northern and southern hemisphere) and *Todarodes filippovae* (only in the southern hemisphere). *Thysanoteuthis rhombus*, a large size but commercially a minor oceanic squid, is also included in the warm water type group.

Octopus vulgaris, *O. aegina* and *O. macropus* are also common over the region but do not appear to be concentrated in any specific locality.

2.2.2 Biological features and applicable fishing gear

A few important items of biological features for the major cephalopod species are summarized in Table 3. The table includes the applicable (currently being applied and assumed to be applicable in the future) fishing gears which are closely linked to the behaviour of each species. It should be noted here that some inconsistencies are involved in the data listed as they were cited from various source documents. It should also be noted that (1) the sizes of a few specific species taken by fisheries are different by localities and fishing gear and (2) the spawning season varies largely by localities. For instance, the spawning season has been studied mostly in temperate waters but little information is available on the tropics. It is not clear, therefore, whether the spawning in tropical waters takes place at the same period in temperate waters. In the tropics the season could be expected to be more prolonged, with multiple spawning occurring.

Cuttlefish

Sepia latimanus is the largest species in the cuttlefish group which grows up to 50 cm mantle length (ML) followed by *S. apama*, 45 cm ML, (Okutani 1980). *S. pharaonis*, *S. lycidas* and *S. aculeata* are also large cuttlefish which fetch a high price. *S. kobiensis* and *Sepiella inermis* are, in contrast, small but are abundant and important to the South Asian and Indian fisheries (Okutani 1980). It is interesting to see that the spawning of *S. inermis* takes place all the year round in Indian waters (Silas *et al.*, 1982), but the spawning of *S. kobiensis* is not known. Many cuttlefish aggregate densely in shallow waters during their spawning season and are effectively caught by traps and trawls. A typical example is shown in the catch of *Sepiella japonica* in the East China Sea (Dong 1981). Analysis of the catch of *S. japonica* shows a strong positive correlationship between the catch and the frequency/magnitude of typhoons attacking the East China Sea during the fishing season (Yu 1981, Chen 1982). Details on the mechanisms and process of the relationship are not clear. However, aggregation of cuttlefish may have been accelerated by some changes in the environment caused by typhoons.

Neritic Squid

Neritic squid in the region generally show a strong aggregative nature which boosts effective fishing by jigging, seining and trawling. In the waters around Hong Kong many squid aggregate during spring to summer (Voss and Williamson 1971, Okutani 1980) but the

Table 3

Biological features and applicable fishing gear for the major cephalopods in the Indo-Pacific region
(the notations in parentheses are assumptions)

Species	Biological features						Applicable fishing gear[d]
	Size[a]		Depth of habitat (m)	Spawning[b] season (month)	Aggregative nature	Phototaxis[c] or cryptic behaviour	
	Mantle length (cm)	Body weight (kg)					
Cuttlefish							
S. pharaonis	20-30	1-4	30-100	3-5	moderate		T,R,P,S,(H)
S. lycidas	20	1-1.5	60-100	3-5	weak		T,R,P,S,(H)
S. aculeata	23	1.3	60	3-5	weak		T,R,S,H
S. ricurvirostra	17	0.4	50-140	?	moderate		T,S
S. latimanus	20-30		5-50	2-10	weak		T,P
S. esculenta	18	0.6	10-100	3-7	strong		T,H,R
S. kobiensis	7			?			T,S
S. apama	20-30		shallow	10-12			T,F,R,H
S. prashadi	14			?			T,S
Sla. japonica	20	0.8		5-6	strong		T,R,H
Sla. inermis	5-8			all around[e]			T,S
Neritic squid							
L. edulis	15-25			4-6	strong	P.strong	F,S,H
L. chinensis	10-30		30-170	2-5,-8-11[f]	strong	P.strong	T,D,C
L. singhalensis	30-40	0.8-1.5	30-170	?	strong		T,S
L. duvaucelii	10-20	0.04-0.2	30-100	all around[e]	strong	P.strong	T,H,S,J
L. japonica	10		shallow	3-7	strong		T,F
L. uyii	10		shallow	?			T,S
Sep. lessoniana	20-30		shallow	5-6		P	T D C S H R G
Sep. australis	38		shallow	?			J,H,F,L
Tod. pacificus	20-30	0.3-0.8	wide area	10-5	strong	P.strong	J,H
No. philippinensis	30		200-600	?			T,S
No. gouldi	20-30	0.2-0.8	40-150	2-3, ? [g]	strong	P.strong	J,T
Oceanic squid							
Ony. banksii	25-35	0.3-0.8	surface[h] layer in open sea	?	weak	(P.)	(J),(G)
Omm. bartrami	30-40	0.8-1.8		10-5	strong[i]	P.(strong)	J,G,H
Sym. oualaniensis	25-40			all around	weak	P.	J,G
Tod. filippovae	20-40			?		P.(strong)	J,(G)
Octopus	Total L.						
O. vulgaris	40-60	0.3-0.6	shallow area	4-5, 9-10	none	P.strong	R,H
O. aegina	30			?	(none)	(P.)	(R),(H)
O. macropus	70			?		(P.)	(R),(H)
O. ocellatus	20-30	0.1-0.2		12-2	none	P.strong	R
O. tetricus	70	0.7		?	(none)	P.strong	R,(H)
Cy. indicus	?			?		(P.)	(R),(H)

a/ Sizes are different by localities and gear, octopus are shown in total length

b/ Spawning is also different by localities

c/ Phototaxis is for cuttlefish and squid, while cryptic behaviour for octopus; P: positive

d/ T: trawl; J: jig; H: hook and line; S: seine; F: fixed set-net; R: trap; G: gillnet; P: spear; D: dipnet; L: troll; C: cast-and-scoop net ("seine" includes the various types of purse seines with and without luring light, beach seines and encircling/surrounding nets with and without light)

e/ Reported from Indian waters

f/ Reported from the Gulf of Thailand

g/ Probably twice

h/ Probably mid-layers (100-200 m) in daytime

i/ Limited to the specific environmental condition cause of this behaviour possibly due to spawning or feeding is not clear. It is interesting to see that *Loligo duvaucelii*, which is a small-size squid but highly abundant and commercially important throughout the tropical region, spawns all the year round in Indian waters (Silas *et al.*, 1982). It also says in the same report that *L. edulis* and *Sepioteuthis lessoniana* spawn twice a year, spring and summer while the latter species in temperate waters is reported to spawn once a year (Okutani 1980). It is assumed that the spawning season may vary greatly by localities and this must be one of the most important items to be studied in the future.

Another notable character of neritic squid is their strong positive phototaxis. Light attraction by torches or small lamps has been traditionally employed to catch squid in many fisheries in the tropical countries, e.g., for purse seining and dipnet in the Philippines (Simpson 1978, 1979, Hernando and Flores 1981), for cast net, dipnet, hook and line along the both coasts of Thailand (Sakurai 1974, Chotiyaputta 1982), and for encircling net in Indonesia (Unar and Sahabi 1982). Although the species taken by these fisheries are not clear, they are likely to include *L. duvaucelii*, *L. chinensis*, *L. edulis*, *L. singhalensis* and *S. lessoniana*. The result of the exploratory jigging recently carried out along the west coast of Thailand, where no intensive light fishing has been performed by local fishermen, confirmed that *L. chinensis* in the area were easily attracted by light and jigging (Shibata, Masthawee and Kitagawa 1980a, Shibata and Masthawee 1980b). It is notable that although the bulk of the squid catch in the tropical area is taken by trawling, nevertheless the squid show behaviour that favours capture by other fishing gears. The degree of phototaxis of the smaller squids, (*L. japonica* and *L. uyii*) is not clear.

The southern species, *Nototodarus gouldi* has been more recently confirmed to have strong positive phototaxis and aggregative nature through exploratory fishing (JAMARC[1/] 1978, 1980, NAFCAJ[2/] 1979, Dunning 1982). The length composition of *N. gouldi* caught by exploratory fishing shows a wide range, which suggests the existence of different groups (at least two) with different spawning seasons though one of them is estimated to spawn during February-March (JAMARC 1980). The future study in connection with the identification of the unit of the stocks is required.

Oceanic Squid

Oceanic squid occurring in the region are a large-size group, especially *Ommastrephes bartrami* which is the largest, reaching 40-50 cm ML or 2-3 kg. *O. bartrami* were caught in substantial amounts by an exploratory drift gillnet fishing at night in the waters midway between Australia and New Zealand, and many specimens were observed swimming on the surface of the sea at night and jigged by the crew of the research vessel (Collins and Dunning 1981). This information confirms the aggregative nature and positive phototaxis of the species on the surface of the sea at night. The massive catch of *O. bartrami* by jigging in the waters along the northern coast of Japan, which falls outside the region, also shows clear evidence of how the species behave. However, the aggregation pattern appears to be different between these two waters - northern and southern Pacific Ocean - in connection with the difference in oceanographic conditions (Murata and Ishii 1977, Okutani 1977). It is reported that *Symplectoteuthis oualaniensis*, a warm water type oceanic squid also shows positive phototaxis and an aggregative nature. It has been commercially caught by hook and line with light at night in the waters around Okinawa to Taiwan, Province of China (Tung, Lan and Hu 1973, Tung 1978a, Yoshikawa 1978, Okutani and Tung 1978, Okutani 1980). It was also caught by jigging with light at night by a Japanese research vessel in the northern Arabian Sea which is bordering on the region in the west (Yamanaka, Nishikawa and Morita 1976, Yamanaka, Yukinawa and Nakamura 1977). The sizes of the squid caught covered a wide range (24-50 cm ML in 1976 and 18-36 cm ML in 1977). They appeared to be some 120-200 m deep in the daytime but moved up to the surface and near surface layers at night, where they could be lured by light and eventually easily jigged. Such diurnal vertical movement is common among pelagic cephalopods including oceanic squid as reported by Roper and Young 1975.

[1/] JAMARC: Japan Marine Fishery Resource Research Center

[2/] NAFCAJ: National Federation of Fisheries Cooperative Association of Japan

Todarodes filippovae were also jigged at night as a by-catch of *N. gouldi* around Tasmania and midway between Australia and New Zealand (JAMARC 1980, Collins and Dunning 1981). The size of the squid caught from the former area was rather small, 17-20 cm ML (JAMARC 1980) but it is not clear for the latter. Not much is known about *Onychoteuthis banksii*.

Octopus

Very little is known about octopus occurring in the region. Detailed information is only available for *Octopus vulgaris* and *O. ocellatus* in the waters around Japan (Aoki *et al.*, 1965, Itami 1975) which falls outside the region. While the former species is cosmopolitan and is distributed all over the world including the region, the latter is a local species in the waters around Japan to the East China Sea. These two species inhabit both sandy and rocky sea bottoms in shallow areas and display a strong cryptic nature which enables fishermen to catch them by traps (pots). *O. vulgaris* is a voracious feeder and is easily captured also by hook and line while *O. ocellatus* are caught almost exclusively in Japan by small traps made of various material, e.g., spiral shells.

Another report on the cryptic behaviour was reported for *O. tetricus* along the west coast of Australia where exploratory fishing by traps made of polyvinyl chloride tubes succeeded recently in catching them in quantities (Anon 1980, a, 1981). *O. tetricus* appear to have voracious feeding habits and to prefer a rocky area judging from the frequent damage by them on the rock lobster pot fishery in the area (Anon 1980).

Information on the other species is very sparse especially in tropical waters of the region. It is assumed that octopus in these tropical waters may inhabit both rocky and sandy bottoms, judging from the substantial by-catch by Thai trawlers (Table 6) and the records on reef fishing in Indonesia (Unar and Sahabi 1982) and the Philippines (Voss 1973). They may also have a strong cryptic behaviour (Jones 1970) and voracious feeding habitat which would make trap and hook and line fishing applicable to those species.

3. FISHERIES AND THE STATE OF EXPLOITATION

3.1 Assessment Methods

Although the assessment of cephalopods may be carried out in broadly the same ways as for fish stocks (IPFC 1982), special problems may arise mainly from the species specific ecological features of the cephalopods involved. These include problems arising from the complexity of stocks and races, their intermingling, highly mobile nature in both horizontal and vertical space (except of course, the octopi), strong aggregative behaviour during spawning and feeding periods, strong phototaxis or cryptic behaviour, short life-spans, etc. These characteristics mainly affect the availability of cephalopods to commercial fishing in complex combinations between the species sought and the fishing gear employed, which means that it is generally difficult to obtain suitable catch and effort data, even from the aimed fishing by trawling or jigging, which can be considered representative of the abundance or density of the stocks concerned.

Apart from these general problems, the serious lack of information on both the biology of cephalopods and their fisheries to date has made the application of traditional assessment methods extremely difficult for the stocks of cephalopods in this particular region. For example, data on fishing effort are almost exclusively unavailable. Even the identification of species is still incomplete in most Indo-Pacific areas, so that the species breakdown of commercial catch has seldomly been attempted by most nations concerned, and even the separation of commercial catches into those of cuttlefish, squid and octopus is not available for many countries. This paucity of information is the representation of the underdeveloped status of cephalopod fisheries in the region as a whole which will be discussed in detail for each sub-area in the following sub-sections.

Under the circumstances discussed above the assessment of cephalopod stocks by traditional methods has been scarcely attempted in the region so far. The only exceptional attempt was that made for squid stocks in the Gulf of Thailand and the Thai waters in the Andaman Sea, by applying a production model to the trawl survey data collected by the Thai research vessels (Chotiyaputta 1982). Even in this case, it is noted that all the squid species (stocks) involved were combined but that the maximum sustainable yield (MSY) estimated for each area referred only to those of demersal type (trawlable) squids. Pelagic squids were excluded from the assessment and will be discussed in detail in the later sections in this paper.

Bearing this background in mind the author found it necessary to apply a semi-quantitative and an independent approach to the assessment of the cephalopod resources (by species group and by sub-area) of the region in this study. A judgment was made as to the abundance and the state of exploitation of a particular resource, bearing in mind (1) the size of the sea areas fished - both horizontal and vertical -, (2) the extent of promising unfished areas for expansion of new fisheries, (3) the number and types of gears used, (4) fishing gears and methods which have not yet been employed in the waters but could be newly introduced there, (5) the possible magnitude of fishing by such new gears and methods, (6) comparison with other species in the same species group in the area and with those in the other areas, (7) information on the stomach contents of predators, and (8) extrapolation and interpolation from better known areas and grounds. The potential yield of total neritic cephalopods in each sub-area has accordingly been estimated on a conservative basis, based on all these. However, it appeared to be premature at this stage to estimate the potential yield of oceanic squid.

The author recognizes that this approach is rather intuitive and will only result in indications as to the stock size and the state of exploitation. At the same time, however, nothing will be done to contribute to rational development of the cephalopod fishery in the region if we have to wait for the accumulation of enough data to carry out conventional analyses, and it may take a considerably long time to obtain such data. The author believes that his conclusions offer first-stage guidelines for development and management purposes. As recommended in the last part of this paper, studies should be initiated on a high priority basis, in order to establish a firm foundation for the rational utilization of cephalopod resources in the region.

3.2 Area Reviews

3.2.1 Yellow Sea and East China Sea

In terms of catch this area has been one of the most important sub-areas in the region (Table 1). Most of the catch is taken by Chinese vessels, about 60 percent by vessels from mainland provinces, and about 30% from Taiwan, Province of China (Table 4). Most of the Taiwanese catch is taken by trawlers extending widely on the continental shelf along almost the entire coast of China, with the exception of the Yellow Sea (DFRCT[1] 1972, 1976, 1977, 1978, 1979, 1980). Although the component of the Hong Kong catch is rather small, 5-7 percent of the total, cuttlefish and squid are of importance and the fishing has been intensively carried out by various gears in the waters around Hong Kong. Statistics from the mainland provinces of China have been reported exclusively as squid. However, this must include both cuttlefish and squid and the catch of the former must be prominent in the total catch judging from a number of reports (Dong 1981, Yu 1981, Chen 1982, Li and Dai 1982). In these papers it is reported that about 30-70 000 t of *Sepiella japonica* were caught in the East China Sea. The author divided the FAO statistics for China into cuttlefish and squid with a ratio of 0.8 and 0.2 respectively. It should also be noted here that the FAO statistics of squid reported from Taiwan, Province of China includes 3-5 000 t of *Ommastrephes bartrami* catch taken in the waters along the northern coast of Japan since 1977 which falls outside the region (Tung 1981).

Cuttlefish

The catch of *Sepiella japonica* is prominent as mentioned above which supposedly accounts for 70-80 percent of the total cuttlefish catch in the sub-area. The bulk of the catch (about 80 percent) is taken by Chinese trawlers (from both the mainland and Taiwan, Province of China) mostly in the western central East China Sea including the Formosa Strait (Dong 1981, Yu 1981, DFRCT 1972, 1979, 1980). Traps (hoopnet with crab bait), offshore setnet and sail dragnet share the rest of the catch which operates mostly when *S. japonica* aggregate densely on the shallower part of the continental shelf during the late spring - summer (Chen 1982, Li and Dai 1982). The catch by trawlers in China increased greatly since

---

[1] DFRCT: Demersal Fish Research Center, Taipei, Taiwan, Province of China

1975 and it is said that the decline in the stock abundance of large yellow croaker caused a shift in the target species of trawlers to *S. japonica* especially during April-June (Yu 1981). The annual catch fluctuates greatly within the range of 30 000-70 000 t. A positive correlation exists between the amount of catch and the magnitude of typhoons (wind velocity) which attacked the East China Sea during the early summer (Chen 1982) but the reason for the phenomenon is not clear. The major stocks in the area appear to have been fully exploited since the early 1960s. Though the annual catch fluctuates considerably there is no obvious trend suggesting a serious impact of too intense fishing.

Table 4

Catch of cephalopods by species group and country in the Yellow Sea and East China Sea, including the northwestern South China Sea along the coasts of China, Taiwan, Province of China and Hong Kong ('000 t)

Special group/ Country	1970	1975	1976	1977	1978	1979	1980	1981
Cuttlefish								
China[a]	45	33	29	32	50	72	64	23
Taiwan	8	11	13	15	17	16	19	19
Hong Kong	1	2	2	2	2	2	2	2
(Sub-Total)	(55)	(46)	(44)	(49)	(69)	(90)	(84)	(43)
Squid								
China[a]	11	8	7	8	12	18	16	6
Taiwan	8	2	23	17	16	30	26	26
Hong Kong	3	5	6	4	5	6	4	5
(Sub-Total)	(22)	(15)	(36)	(29)	(33)	(54)	(46)	(37)
Octopus								
China	?	?	?	?	?	?	?	?
Taiwan	1	1	1	1	1	1	1	1
Hong Kong	?	?	?	?	?	?	?	?
(Sub-Total)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)
Total cephalopods	78	62	81	79	103	145	131	81

[a] Estimated by the author from FAO Statistics (see text)

Table 5

Catch of cephalopods by species group and country in the waters around the Philippines ('000 t)

Species group/ Country	1970	1975	1976	1977	1978	1979	1980	1981
Cuttlefish								
Philippines	0	1	1	1	5	2	3	3
Squid								
Philippines	17	30	24	25	26	25	27	28
Octopus								
Philippines	1	2	2	1	1	1	2	1
Total cephalopods	18	32	26	27	32	29	32	32

Sepia esculenta is the next important species in terms of the amount of catch in the area. It is distributed in the entire sub-area extending to the South China Sea. However, the larger catch (about 10 000-20 000 t annually) is taken in the Yellow Sea to East China Sea by the Japanese, Korean (Rep.) and Chinese trawl fisheries, of which the Chinese catch is estimated to be 1 000-2 000 t (Dong 1981). Other gears employed are traps, fixed setnet and hook and line. As with *S. japonica*, the species aggregate in a shallow area during the spawning season, March-July and are then caught in large numbers (Okutani 1980). These northern stocks, which extend to Korean and western Japanese waters, appear to have been fully exploited since the late 1950s. Fishing on the southern stocks is not clear but this is believed to be one of the important species off the southern coast of China (including Taiwan). The catch composition of the Taiwanese trawlers operating in the Formosa Strait and along the southern coast of China show that cuttlefish are ranked from first to sixth among the species caught with 5-10 percent of the total catch (Liu and Kao 1979, DFRCT 1978, 1979, 1980). The cuttlefish catch around Hainan Island by the Taiwanese trawlers is some 0.7-2.5 percent and ranks tenth to thirteenth (DFRCT 1978, 1979, 1980). Details on the species of these catches are not available. However, there is no doubt that *S. esculenta* is included as one of the major components.

The three larger species of commercial value, *Sepia pharaonis*, *S. lycidas* and *S.aculeata*, may also be included in the Chinese trawl catch as both mainland and Taiwan) in the East China Sea and further south. These species are caught mostly as by-catch by trawlers and other gears and are not caught in large quantities while *S. pharaonis* are trapped or speared in Hong Kong when they aggregate in shallow areas during the spawning season, March-May. *S. recurvirostra*, a smaller species also comprises a component of the trawl catch in the central to southern area, especially around Hong Kong (Voss and Williamson 1971, Okutani 1980). These four species may comprise several local stocks and the exploitation on them is rather intense due to high commercial value.

S.latimanus, the largest species which is widely but sparsely distributed, further intensified catching is therefore difficult. Not much is known about the commercial fishing of the smallest species *S. kobiensis*. Although this species is widely distributed in the area it may be only locally utilized due to its low commercial value with small size (7 cm ML) and much black ink contained (Aoki *et al.*, 1965, Okutani 1980).

Neritic Squid

Squid resources in the sub-areas generally appear not to have been intensively utilized by China (Dong 1981) but the Taiwanese and Hong Kong fisheries have been quite active (Table 4). The catch record of the Taiwanese trawl fishery shows two major productive areas, one in the southwest of Formosa Strait and the other in the western East China Sea (DFRCT 1976, 1977, 1980), which may be composed of different species.

Todarodes pacificus, a northern and large-size species, is distributed in the East China Sea, where major stocks in the Northwest Pacific spawn, and in the Yellow Sea and further north. It is well known that the stock has been intensively and fully exploited by the Japanese and Korean fisheries in the waters around the Korean peninsula and Japan including the above-mentioned area in the region (Okutani 1977). It appears, in spite of its abundance, that the utilization of this species by Chinese fisheries is very low, probably negligible in the mainland provinces and only a small amount of by-catch by trawlers from Taiwan in the East China Sea.

The species in the area which are currently exploited are *Loligo chinensis* and *L. edulis*, both are medium-sized squid (Table 3), and are distributed commonly over the Indo-Pacific region (Table 2). The Chinese landings in the mainland provinces of these two species were reported to be about 10 000 and 6 000 t respectively (Dong 1981), together probably accounting for the majority of the Chinese squid catch (Table 4). *L. chinensis* are intensively exploited also by the Hong Kong fishery, especially during July-September and are said to account for about half (2 000-3 000 t) of the total squid catch by Hong Kong (Voss and Williamson 1971, Okutani 1980). It is assumed that the catches by the Taiwanese trawlers in the southwest of the Formosa Strait already mentioned may comprise mostly *L. chinensis*.

A northern small-sized squid, *L. japonica* is caught in the Yellow Sea and East China Sea, and the Chinese catch is reported to be several thousand tons (Dong 1981). The catches by Taiwanese trawlers in the East China Sea may be a mixture of *L. edulis*, *L. chinensis* and *L. japonica*.

Most of the squid species in the area are caught by trawl, both aimed in the specific season (July-September in Hong Kong) and by-catch in the others. However, aimed purse-seing is employed in Hong Kong during May - September for catching *L. duvaucelii* and *S. lessoniana* (Okutani 1980, Shin 1982).

It appears that the squid stocks in the area are generally moderately exploited with the exception of *T. pacificus* in the north, since pelagic stocks have been scarcely harvested.

Oceanic Squid

It is on record that *Symplectoteuthis oualaniensis* are caught commercially in the eastern and southern East China Sea, Taiwan to Okinawa, by hook and line with light at night (Tung 1978, Yoshikawa 1978, Okutani and Tung 1978, Okutani 1980). The annual catch of *S. oualaniensis* has been about 300-400 t. No record on the commercial catch of *Ommastrephes bartrami* has been reported from the sub-area.

Octopus

Information on octopus in the sub-area is seriously limited (Table 4) though a few species are believed to be common in the area (Table 2). It is said that in addition to the by-catch of trawlers, traps are used in China in a few limited local areas and that in Hong Kong and Taiwan, Province of China both traps and hook and line are also used to catch octopus. The stocks are supposedly only slightly exploited judging from the small catches currently taken in comparison with the vast extent of possible habitat in the sub-area and the high production along the neighbouring coasts, western Japan and the Republic of Korea.

3.2.2 Waters around the Philippines

Although cuttlefish and squid appear to be distributed abundantly along the entire coast and to have been utilized widely by various types of fisheries (Voss 1963, 1973), fishing has not been intense and the biological information on these species is very poor, e.g., the species in of the catches have not been fully identified. This was generally accepted at a series of workshops on fishery resources around the Philippines organized by the FAO/UNDP South China Sea Fisheries Development and Coordinating Programme (SCSFDCP). The workshop recommended, based on the findings, that biological studies should urgently be made of the major species (SCSFDCP 1976, Simpson 1978, 1979).

Cuttlefish

The reported catch of cuttlefish is very small though it shows a gradual increase since the mid-1970s (Table 5). Cuttlefish are mostly caught by the small-scale fisheries. Many types of gear are used including hook and line, seine-net, gillnet, traps, liftnet and various types of indigenous fishing gears, of which the first two took the majority of the catch with about 70-80 percent of the total (SEAFDEC[1] 1980, 1981, 1982). About 65 percent of the total catch is taken by the hook and line of the small-scale fishery in the Mindanao area. Catches in the large-scale industrial fishery is limited to trawling in the Luzon area and is very small accounting for only about 5 percent of the total.

The main species are probably *Sepia pharaonis*, *S. lycidas* and *S. esculenta* with smaller catches of *S. aculeata*, *S. recurvirostra* and *S. latimanus* and probably others (Table 2). All the species may be composed of a number of local stocks. It appears that the inshore stocks in most areas may have been generally heavily exploited by the small-scale fisheries, especially in Luzon and Mindanao. However, the production from the central and western part of the sub-area, the Visayan Sea and the Sulu Sea along the Parawan Islands, has been very low with less than 10 percent of the total cuttlefish catch in the Philippines. It is believed that the stocks in these areas may have been not heavily fished when the vast extent of possible habitat there is taken into account. The potential harvest of cuttlefish in the waters around the Philippines would therefore be greatly larger than the present catch.

---

[1] SEAFDEC: Southeast Asian Fisheries Development Center, Bangkok, Thailand

Neritic Squid

Catching squid in the Philippines is more intensive than catching cuttlefish but the annual catch has been rather stagnant since the mid-1970s (Table 5). Fishing grounds extend widely along the entire coast with the exception of the Moro Gulf, Tawi Tawi Islands and the Sulu Sea side of the central Philippines (Hernando and Flores 1981). In contrast to the cuttlefish catch, large-scale fishing accounts for about 50 percent of the total squid catch of which trawlers in Luzon and Visaya (the central Philippines) areas account for about 40 percent (SEAFDEC 1980, 1981, 1982). The catch by the small-scale fishery, which accounts for about 50 percent of the total, is achieved by various types of indigenous gears such as hook and line, liftnet, gillnet, purse and beach-seine, surrounding net, scoop net and jigging, of which the first two account for more than 50 percent of the total catch of the small-scale fishery. It is said that liftnet is a totally night fishing gear with light while encircling net and purse seine are operated both in the daytime and at night with luring light (Hernando and Flores 1981) but it is not clear whether light luring is employed in hook and line fishing.

The main species in the catch are believed to be *Loligo duvaucelii* and *L. edulis* with small catches of *L. chinensis*, *L. singhalensis*, *Sepioteuthis lessoniana* and *Nototodarus philippinensis* (Table 2). It is surprising that trawlers catch most squid, despite the rather limited trawlable area in the Philippine waters. This suggests that the other methods for fishing squid are not well developed, and that the potential harvest of squid in the area would be much larger than the present catch.

Oceanic Squid

Although three species of oceanic squid, *Onychoteuthis banksii*, *Ommastrephes bartrami* and *Symplectoteuthis oualaniensis* are believed to inhabit the sub-area (Table 2), no information on catching any of these species has been reported. On the analogy of the substantial catch of *S. oualaniensis* by hook and line in the waters around Okinawa where the Kuroshio, a large warm water current prevails, the same species could be distributed in the sub-area especially in the waters along the northern and eastern Luzon at the beginning of the Kuroshio. Future surveys on both the biology of the species and the oceanographic conditions there are required to examine this. *O. bartrami* may be the least abundant as the area is located at the southern margin of the distribution of this species.

Octopus

Catch of octopus is very small (Table 5) and no substantive information on the species caught and the fisheries is available. A few species appear to inhabit the area but the fishing on them has been limited. It is said that octopus are usually caught on reefs by hand at night with the aid of torches (Voss 1973) but the torches may be used to locate the target and not to lure.

3.2.3 South China Sea

As defined previously the sub-area employed in this paper excludes the waters along the mainland coast of China and around the island of Taiwan. The catch by species group and country in the sub-area is given in Table 6, but the production by Kampuchea is completely unknown though it has probably been very small over the past decade due to the disturbances there. The recent catches of Viet Nam are also unknown. The annual total cephalopod production of Viet Nam, estimated by FAO based on extrapolation for earlier data, were divided into those of cuttlefish and squid with 50 percent for each and presented in Table 6.

Bearing the intensity of fishing by different national fleets in mind, it appears that the state of the exploitation of cephalopod resources in the sub-area is different among the four major localities, the Gulf of Thailand, Malacca Strait, Sunda Shelf and the central part of the South China Sea. The resources are probably most heavily exploited in the first, less in the second and third, with virtually no exploitation in the last.

3.2.3.1 Gulf of Thailand: Among the countries bordering the area, only information on the Thai fisheries is available. However, there may not be a large error in depending only on the Thai information as the species composition, and the biological features of the resources are believed to be quite similar in the Kampuchean and Vietnamese waters, and the Thai trawlers have fished intensively in those waters.

Table 6

Catch of cephalopods by species group and country in the South China Sea, including the Gulf of Thailand and Malacca Strait but excluding the waters along the coasts of China, Taiwan, Province of China and Hong Kong
('000 t)

Species group/ Country	1970	1975	1976	1977	1978	1979	1980	1981
Cuttlefish								
Viet Nam[a]	2	7	7	7	7	7	7	7
Kampuchea	?	?	?	?	?	?	?	?
Thailand	12	25	23	30	31	20	23	21
Malaysia	4	8	13	14	17	5	4	5
Singapore	0	0	0	0	0	0	0	0
Taiwan[b]	3	1	2	1	1	0	1[c]	1[c]
(Sub-Total)	(21)	(39)	(45)	(51)	(55)	(38)	(35)	(33)
Squid								
Viet Nam[a]	2	7	7	7	7	7	7	7
Kampuchea	?	?	?	?	?	?	?	?
Thailand	21	37	35	47	47	37	36	33
Malaysia	1	1	1	1	1	12	9	12
Singapore	0	0	0	0	0	0	0	0
Taiwan[b]	1	0	0	0	1	1	1[c]	1[c]
(Sub-Total)	(26)	(45)	(43)	(55)	(56)	(57)	(53)	(53)
Octopus								
Viet Nam	?	?	?	?	?	?	?	?
Kampuchea	?	?	?	?	?	?	?	?
Thailand	1	3	4	7	7	7	6	5
Malaysia	?	?	?	?	?	?	?	?
Singapore	?	?	?	?	?	?	?	?
Taiwan[b]	0	0	0	0	0	0	0[c]	0[c]
(Sub-Total)	(1)	(3)	(4)	(7)	(7)	(7)	(6)	(5)
Total cephalopods	48	87	92	113	118	102	94	91

a/ Estimated by the author from FAO Statistics (estimates), see text

b/ Long-range pair trawl fleet

c/ Estimated by the author, average during 1978-79

Cuttlefish and Neritic Squid

The bulk of the catch of cuttlefish and squid in the Thai fisheries is taken by trawlers (both otter and pair trawlers) of the large-scale fishery, usually more than 95 percent of the total for cuttlefish and 85 percent for squid (Sakurai 1974, SEAFDEC 1980, 1981, 1982). Other fishing gears employed in the cuttlefish fishery are bamboo stake trap, push net and cast net while a greater variety of gears are employed in squid fishing, including the above-mentioned three gears, as well as luring purse seine, gillnet, cast net scoop net and hook and line. In the small-scale fisheries the cast net is prominent producing about 8 percent of the total squid catch, including that by large trawlers (SEAFDEC 1981, 1982). Light luring is also used with scoop net, hook and line and liftnet catching for squid (Sakurai 1974, Chotiyaputta 1982). It is reported that electric lamps with 3-12 kw generators are gradually substituting the traditional light luring methods with torches or kerosene lamps and that this modernization is recently accelerated with the conversion of trawlers into squid fishing boats due to the falling catch rates in finfish trawling (Chotiyaputta 1982).

The species composition of cuttlefish taken by the Thai fisheries is not clear but Sakurai (1974) reported that there are four distinct major species. They are supposedly *Sepia recurvirostra*, *S. pharaonis*, *S. lycidas* and *S. aculeata*. The other minor species to be taken may be *S. latimanus*, *S. kobiensis* and *Sepiella inermis* (Table 2).

The major species in the catch of squid are reported by Chotiyaputta (1982) to be *Loligo chinensis* (15-40 percent of the trawl catch), *L. duvaucelii* (10-16 percent of the trawl catch) and *Sepioteuthis lessoniana* (9-12 percent of the trawl catch). It should be noted that the sizes of these species are considerably smaller (*L. chinensis*: 9-10 cm ML, *S. lessoniana*: 10-14 cm ML) than commonly observed in the northern region (Table 3). The minor species taken by the various types of gears may include *L. edulis*, *L. singhalensis*, *L. uyii* and *Nototodarus philippinensis* (Table 2).

The catch of cuttlefish and squid by the Thai fisheries has steadily increased during the mid-1960s to the early 1970s. Sakurai (1974) assumed that there are two major reasons for this; firstly, that the abundance of cuttlefish and squid might have increased in combination with the decline in the demersal fish stocks due to the heavy fishing by trawlers during the period, and secondly, that directed fishing on cuttlefish and squid had been expanded to meet the increase in the demand for these products for domestic consumption and for export. There would not be any question on the second reason but there would be some on the first. It is well known that many demersal fish stocks in the Gulf of Thailand were depleted during the first half of the 1960s (SCSFDCP 1978, a). Nevertheless, the catch per unit effort (cpue) data collected by the research vessel during the period shows a fairly stable trend for cuttlefish and a substantial increase for squid in contrast to the large decrease in many finfish and the total catch (Ritragsa 1976). Pauly (1979) analysed these data and categorized them into three groups, i.e., (1) species showing a significant decrease, these include many finfishes and (2) species with no significant change, this includes cuttlefish and (3) species which show a significant increase, this includes squid. Sakurai's assumption on the change in species composition must be true on squid stocks but not so clear on cuttlefish stocks.

Chotiyaputta (1982) estimated the MSY of squid in Thai waters in the Gulf of Thailand, based on the trawl survey data, to be about 42 000 t and that the fishing may have reached the maximum level in 1977 but this may be doubtful as squid stocks are not thoroughly dependent on the bottom of the sea and these are not fully vulnerable to bottom trawling. Potential harvest of cuttlefish and squid is supposed to be larger than the present catch when the proportion of these species occurring in mid-water, and around the widely distributed small island areas, especially along the Kampuchean and Vietnamese coasts where trawling may be unsuitable, are taken into account. In any case, if Pauly's conclusions are correct the potential annual yield of squid will depend on the pattern of fishing on the demersal finfish, increasing when the latter stocks are depleted.

Oceanic Squid

There may be no large possibility of harvesting oceanic squid in the area, which includes no deep water oceanic areas.

Octopus

The catch of octopus has been reported only from Thailand, where it is almost entirely taken by trawlers as by-catch. The stocks may have been only slightly exploited and further increases in the catch may be possible if other fishing methods such as traps or hook and line can be used on the several species in the area which presumably occur (Table 2).

3.2.3.2 Sunda Shelf: The Sunda Shelf is bordered by Viet Nam in the northwest, the Gulf of Thailand in the west, Malaysia (the east coast of the Malaysian peninsula) in the southwest, Indonesia (the southeast coast of Sumatra and the west coast of Kalimantan) in the south, Sarawak, Sabah and Brunei in the east and the deeper central South China Sea in the northeast. The cephalopod resources have generally been only slightly exploited in the area.

Information on cephalopods in the area is very scarce generally due to the absence of fishing on these resources by the coastal nations (Latif 1982, Unar and Sahabi 1982). The Malaysian catch of cephalopods in the area was only about 5 000-5 300 t during recent years of which about 65 percent was taken along the east coast of the Malaysia peninsula and the rest along Sabah and Sarawak (SEAFDEC 1980, 1981, 1982). The Indonesian catch in the area, which is difficult to separate and is included in the total Indonesian catch in Table 7, is presumed to be very small too, 3 000-4 000 t at the most (Unar and Sahabi 1982). The catch by Brunei is negligible if the Vietnamese catch estimated by FAO (12 900 t) is reasonable; the total cephalopod catch in the region is estimated to be about 21 000-23 000 t at the most which appears small in comparison with the extent of the continental shelf in the area. In these circumstances, and also due to the lack of information which resulted from such a state, little attention has been paid specifically on cephalopod resources at a series of workshops on the resources of the Sunda Shelf which concentrated more on finfish and shrimp (SCSFDCP 1978, a,b).

Cuttlefish and Neritic Squid

The results of the trawl survey carried out by Thailand, Malaysia and Indonesia which was summarized at one of the above-mentioned workshops, showed relatively low catch rates for cuttlefish and squid in many waters in the area (SCSFDCP 1978, a). However, records of commercial trawl fishing by the Taiwanese fleet show considerably high catch rates for these species groups during the past decade (DFRCT 1976, 1977, 1978, 1979, 1980; Liu, Lai and Yeh, 1978). For instance, the catch of cuttlefish accounted for 8 to 20 percent of the total which was ranked at second to sixth among the species caught and squid 2-13 percent with a seventh to thirteenth ranking. There is no doubt therefore that cuttlefish and squid are abundantly distributed on the continental shelf of the area and could compose one of the commercially important components of the cephalopod fishery if such a fishery is developed there. It should be noted that the cuttlefish catch was very high in the south of Vietnam. It also appears that catches of cuttlefish and squid by the Taiwanese trawlers are generally lower along the Sarawak and Sabah coasts than in the western part of the area.

Most of the catch of cuttlefish in Malaysia has been taken by the trawlers of the large-scale fishery, usually 70-80 percent of the total cuttlefish catch. However, a substantial amount of the cuttlefish catch has been taken by traps along the east coast of the Malaysia peninsula and hook and line in Sabah (SEAFDEC 1980, 1981, 1982). In contrast, the share of trawler in the squid catch is less accounting for 50-60 percent of the total along the east coast of the Malaysia peninsula and 25-35 percent in Sabah. The rest of the squid catch is taken by purse-seine, traps, hook and line, liftnet and gillnet.

Details on the catch along the Indonesian coast are not known but are presumably the by-catch of the various types of small-scale fisheries (Unar and Sahabi 1982).

No information is available on the species of cuttlefish in the area, however, it is assumed that the species composition would be almost the same as that in the Gulf of Thailand.

Five major squid species were reported from the Malaysian waters, *Loligo duvaucelii*, *L. uyii*, *L. edulis*, *L. singhalensis* and *Sepioteuthis lessoniana*[1] but the relative importance of these species was not given (Latif 1982). It is quite likely that the species composition in the area is similar to that in the Gulf of Thailand. *L. chinensis* and *Nototodarus philippinensis* must, therefore, be taken in substantial quantities in addition to the above-mentioned five species.

Oceanic Squid

No information has been obtained on the existence of oceanic squid in the area but in the absence of deep water it is unlikely that they occur in quantity on the Sunda Shelf.

Octopus

There is no information on octopus from the area, but presumably the density and species composition are similar to that of the Gulf of Thailand. Several hundreds (or thousands) of tons of octopus could therefore be harvested if suitable fishing methods other than trawling are introduced.

1/ Latif (1982) identified this as *Sepioteuthis* spp. but there may be no doubt that the species is *S. lessoniana*.

3.2.3.3 Malacca Strait: Similar to the Sunda Shelf area, the general status of the cephalopod fishing in the area has been rather stagnant (Latif 1982, Unar and Sahabi 1982) and little attention has been paid so far to cephalopod resources (SCSFDCP 1976a, b, 1978b).

Cuttlefish and Neritic Squid

The total catch of cuttlefish and squid from the area in recent years is estimated to be about 11 000-15 000 t, of which 9 000-12 000 t are taken by Malaysia (SEAFDEC 1981, 1982) and 2 000-3 000 t by Indonesia (Anon. 1976a, b, Unar and Sahabi 1982).

The Malaysian catch (3 000-4 000 t of cuttlefish and 6 000-8 000 t of squid) has been mostly taken as a by-catch by trawlers of the large-scale fishery (94 percent for cuttlefish and 97 percent for squid in 1980) and there is no aimed fishing on these resources. The Indonesian catch is also presumed to have been mostly taken by trawlers (Anon. 1976a, b). The major demersal stocks including shrimp in the area have been heavily exploited exceeding the MSY level (SCSFDCP 1978b). However, this may not be applicable to cephalopod stocks in the area because along both the Malaysian and Indonesian coasts much of the stocks is in mid-water, or in the offshore area in the northwest part of the Strait and is less vulnerable to trawling. The potential yield of cuttlefish and squid in the area may therefore be considerably higher than the current catch.

The species composition of the two species groups may be the same as those in the Gulf of Thailand in the south and to that in the Bay of Bengal, which will be discussed in a later section in this paper, in the north.

Oceanic Squid

Oceanic squid are not important in the area.

Octopus

Octopus resources seem not to have been utilized at all in the region though it is reasonable to suppose that they occur in moderate densities. Several hundreds or thousands of tons of harvest could be obtained if the fishing on these stocks is suitably introduced.

3.2.3.4 Central South China Sea: No information is available on the cephalopods in the deeper central part of the South China Sea. A few likely assumptions on this area are: (1) some cuttlefish, squid and octopus stocks may be distributed around the many island groups in the area, and (2) one or two oceanic squid possibly exist on or around banks and seamounts especially in the eastern part of the area, along Palawan to Luzon. However, the feasibility of commercial fishing on these stocks may be lower than the other part of the South China Sea especially from an economic point of view.

3.2.4 Java Sea to northern Arafura Sea

The area comprises Indonesian waters exclusively and includes the Java Sea, Makassar Strait, Sulawesi Sea, Molucca Sea, Ceram Sea, Flores Sea, Banda Sea and northern Arafura Sea. The entire area of these seas is the largest but the information on cephalopods there is the least in the region. The total cephalopod catch from the entire Indonesian waters is shown in Table 7, of which 9 000-10 000 t are estimated to have been taken from this subarea in recent years. This is equivalent to about 10 percent of the total cephalopod catch in the South China Sea (Table 6) where the sea area is nearly the same which shows clearly the probable state of underexploitation of cephalopods in the region. In these circumstances, little attention had been paid by the institutes/scientists to the cephalopod resources in the area until recent years (Buzeta, Dwiponggo and Sujastani 1979). Most of the catch has been taken by the various types of coastal small-scale fisheries and no aimed intensive fishing on cephalopods has been employed so far with the exception of very limited localities and seasons (Unar and Sahabi 1982).

Table 7

Catch of cephalopods by species group and country in the Java Sea to northern Arafura Sea, including the Indian Ocean along the Indonesian coast ('000 t)

Species group Country	1970	1975	1976	1977	1978	1979	1980	1981
Cuttlefish								
Indonesia	1	1	2	2	2	2	2	2
Squid								
Indonesia	7	10	8	7	9	13	11	11
Octopus								
Indonesia	0	0	0	0	0	0	0	0
Total cephalopods	8	11	10	10	10	14	13	13

Cuttlefish and Neritic Squid

The cuttlefish catch from the area is estimated to be about 1 500 t which is probably far below the potential annual harvest. Species to be taken are quite vague but probable species are: *Sepia pharaonis*, *S. recurvirostra* and *S. latimanus* but the relative importance among them is not known. *S. lycidas*, *S. aculeata*, *S. esculenta* and *Sepiella inermis* probably also supposedly occur in the area but this needs future confirmation (Table 2). It is noted that several species of Sepiolidae, which is the smallest-size group of cuttlefish, may be abundantly distributed in the shallower part of the Java Sea where bottom structure and oceanographic conditions are generally favourable for these species.

The species composition of squid is also very vague and the only species confirmed to be taken in a substantial amount in the area is *Loligo edulis*. In the Alas Strait, which is located between the Lombok and Sambawa Islands connecting the Java Sea to the Indian Ocean, aimed fishing on squid with light-lured encircling net is employed during the west monsoon season from September to February. The most common species in the catch was identified as *L. edulis* but the other species included in the catch were not identified (Unar and Sahabi 1982). The other major species probably occurring in the area are *L. duvaucelii* and *L. chinensis*, *L. singhalensis*, *L. uyii*, *Sepioteuthis lessoniana* and *Nototodarus philippinensis* probably also occur (Table 2). However, these assumptions need to be confirmed in the future.

The results of a series of trawl surveys carried out in the Java Sea generally show a rather low catch rate for cuttlefish and squid and the components in the total catch are very small 0.2-2.0 percent for cuttlefish and 2.0-4.9 percent for squid (Martosubroto and Pauly 1976, Losse and Dwiponggo 1977, Beck and Sudradjat 1978, Dwiponggo and Badrudin 1980). This may more or less suggest the low abundance of these species groups in the Java Sea. However, more studies are needed since, as indicated in an earlier section, on the Sunda Shelf commercial vessels fishing specifically for these species found good catches even if the catches in research vessel survey were low.

The Taiwanese trawl fleet caught a substantial amount of cuttlefish and squid from the Savu Sea (south of Flores and west of Timor) and the continental shelf along the Sambawa Islands (southeast of the Alas Strait mentioned previously) in 1976 (DFRCT 1977). The fleet has also been catching a substantial amount of cuttlefish and a large amount of squid from the Arafura Sea (DFRCT 1976, 1977, 1978, 1979, 1980, Liu, Lai and Yeh 1978) where the northern part of the fishing ground, south of Irian Jaya, is included in this sub-area. The total catch of cuttlefish and squid taken by the Taiwanese fleet from the entire Arafura Sea and the waters along the northwest coast of Australia is given in Table 8 which will be discussed in the next sub-section. These records indicate clearly the existence of abundant cuttlefish and squid resources in the southern and eastern parts of the Indonesian waters. The species composition of these resources may be the intermediate type between the South China Sea and northern Australia (Table 2). It is also quite likely that the pelagic form of several species of squid are abundantly distributed in many straits/bays/inlets and waters around the numerous islands along the southern to eastern part of the area.

Table 8

Catch of cephalopods by species group and country
in the waters around Australia
('000 t)

Species group Country	1970	1975	1976	1977	1978	1979	1980	1981
Cuttlefish								
Australia	0	0	0	0	0	0	0	0
Taiwan[a]	–	1	2	2	1	1	1[b]	1[b]
(Sub-Total)	(0)	(1)	(2)	(2)	(1)	(1)	(1)	(1)
Squid								
Australia	0	0	0	0	0	1	1	1
Taiwan[a]	–	8	6	1	4	16	10[b]	10[b]
(Sub-Total)	(0)	(9)	(6)	(1)	(5)	(16)	(11)	(11)
Octopus								
Australia	–	–	–	–	0[c]	0[c]	0[c]	0[c]
Taiwan[a]	–	0	0	0	0	0	0	0
(Sub-Total)	(-)	(0)	(0)	(0)	(0)	(0)	(0)	(0)
Total cephalopods	0	9	8	3	6	17	12	12

a/ Long-range pair trawl fleet

b/ Estimated by the average during 1978-79

c/ Exploratory fishing

Almost no information is available for the northern part of the area, Sulawesi-Molucca-Ceram-Banda-Flores Seas. It is probable, however, that several species of cuttlefish and squid may be substantially distributed along the coasts of countless islands. Species composition may be tropical resembling that of the southern area.

Oceanic Squid

In the northern deep-waters including the Pacific Ocean side, some oceanic squid, possibly *Symplectoteuthis oualaniensis*, *Onychoteuthis banksii* and *Thysanoteuthis rhombus* could be distributed (Okutani 1980).

Octopus

Again, no substantive information is available on octopus resources in the area. Unar and Sahabi (1982) reported that octopus are limited to coral reef waters. However, the author assumes this may refer only to the limited fishing activities on octopus, and that several species must be widely distributed (Table 2) on various types of sea bottom judging from the general biological features of the probable species (Table 3).

Taking all the information and assumptions into account, it is believed that the potential yield of cephalopod resources from the sub-area may be much larger than the present catch, possibly more than an order of magnitude.

3.2.5 Waters around Australia

Waters around Australia are divided into two, the north where a more or less tropical regime prevails, and the south where temperate oceanographic conditions rule. The species composition is accordingly quite different between these two waters (Dunning 1982). Local fisheries on cephalopods is very minor but is steadily developing. The bulk of the commercial catch is currently taken by the Taiwanese trawl fleet (Table 8) from northern waters. The current catch from the entire area is believed therefore to be far below the potential yield.

3.2.5.1 Northern waters

Cuttlefish

Although it is believed that many species of cuttlefish are distributed in the area, *Sepia pharaonis* and *S. latimanus* are the only species to have been reported so far (Okutani 1980, Dunning 1982). The other species may resemble those in the Java Sea to north Arafura Sea (Table 2). The local fisheries on cuttlefish in the area is almost non-existent (Table 8). The catch of cuttlefish by the Taiwanese trawlers is spread widely on the continental shelf along the north to west coast of Australia without any discontinuities and accounts for 1-4 percent of the total catch. It ranks sixth to fifteenth among the species caught (Liu, Lai and Yeh 1978, DFRCT 1979, 1980). The species are therefore probably abundant and the potential harvest along the entire northern coast, including the waters where no commercial fishing is being performed now, may be considerably larger than the present catch.

Neritic Squid

Squid resources in the area are similar to cuttlefish, and are almost exclusively taken by Taiwanese trawlers (Table 8). Species confirmed in the area are *Loligo edulis*, *L. chinensis*, *L. singhalensis* and *Sepioteuthis lessoniana* (Dunning 1982) which resembles that in the neighbouring sub-area, the Java Sea to the northern Arafura Sea. In this connection, *L. duvaucelii* and *L. uyii* may possibly be distributed in the area though their abundance may be low (Table 2). Dunning (1982) reported the occurrence of *Loligo bleekeri* in the area. However, it has been reported that *L. bleekeri* is commonly distributed in the waters around Japan but is rarely found in Indonesian waters (Aoki *et al.*, 1965). There is some doubt, therefore, on whether *L. bleekeri* is commonly distributed in the Australian waters. Another question occurs on the species identification of *L. edulis* as was discussed in the earlier sections. There may be two or three different sub-species involved in *L. edulis* in the area.

Oceanic Squid

Some oceanic squid may inhabit the area but nothing has been confirmed (Table 2).

Octopus

There is no information on octopus in the area, however, several species may be distributed in substantial abundance (Table 2).

3.2.5.2 Southern waters

Cuttlefish

Sepia apama is the only species of cuttlefish confirmed as being commonly distributed along the southern coast of Australia (Okutani 1980, Dunning 1982). However, the catch by local fisheries is very small (Table 8) and abundance of the species is not clear. It is believed that in addition to *S. apama* several medium to small-sized species are abundantly distributed in the area (Okutani 1980) but details are not known. Although Dunning (1982) reported the occurrence of *S. rex* and *S. hedleyi*, further studies are required as the taxonomic status of these two species has not yet been well clarified. The result of an exploratory trawl survey along the southwest coast of Australia shows a substantial catch of cuttlefish there with about 3 percent of the total. Cuttlefish were ranked at eighth among the species caught (Anon. 1982a). As most of the local catch of cuttlefish is taken as by-catch of prawn trawlers in shallower inshore waters (Dunning 1982), a large increase in the total cuttlefish catch could be achieved should suitable fishing methods be introduced.

Neritic Squid

Among the squid resources in the area *Nototodarus gouldi* is abundant especially in the waters around Tasmania and the southeast coast of Australia (JAMARC 1978, 1980, Okutani 1980, Dunning 1982). Exploratory fishing by both the Japanese commercial squid fishing fleet and the Australian research vessel with modern light-lured and mechanized squid jigging has been successful (NAFCAJ 1979, Anon. 1982). It is reported that the Taiwanese squid jigging fishery also operates intermittently in the area and the total annual catch by both the Japanese and Taiwanese fisheries was estimated to be 4 000-8 000 t in recent years (Dunning 1982). The potential harvest of the stock is not known, but may be several tens of thousands of tons.

The other species of squid confirmed in the area is *Sepioteuthis australis* which are reported to inhabit shallower waters being caught by troll, hook and line and setnet (Dunning 1982). There may be several additional species occurring in the area but no information on them is available.

Oceanic Squid

A few oceanic squid have been confirmed from southern waters. *Ommastrephes bartrami* were caught in large quantities by gillnet at night in the waters midway between Australia and New Zealand during the exploratory fishing carried out by a Taiwanese research vessel (Collins and Dunning 1981). A few specimens were also caught by jigging during the same cruise. The catch of *O. bartrami* by jigging was also reported from Tasmanian waters by Japanese jigging vessels for *N. gouldi* (JAMARC 1978, 1980). It is interesting to see that some albacore, *Thunnus alalunga* and skipjack, *Katsuwonus pelamis* were also caught together with *O. bartrami* by the above-mentioned gillnetting. The potential yield of the species appears to be large and commercial exploitation must be feasible. However, the future studies on both the biology of the species and environmental conditions are needed carrying out to confirm this. *Todarodes filippovae*, a typical cold water species around the Antarctic (Okutani 1980) was caught by jigging together with *O. bartrami* (Collins and Dunning 1981) and with *N. gouldi* (JAMARC 1978, 1980). However, information is too sparse to assess the stock and feasibility of commercial fishing.

Octopus

It is quite interesting to see the successful results of exploratory fishing on an octopus, *Octopus tetricus* along the southwest coast of Australia (Anon. 1980, a, 1981). Fishing was originally aimed partly at reducing the damage (predation) on rock lobsters caught in pots and partly at producing an export product from an unutilized resource. Pots made of polyvinyl chloride tube are used and one small exploratory boat (4.8 GT) caught about 18 t (25 700 specimens) during 7 months in 1980 (Anon. 1980a). The fishing ground is quite limited due to the small-scale exploration and the distribution range of the species is not known. However, it is likely that the species inhabits a wide area with a fairly large biomass.

Further information on octopus in the area comes from the stomach content of sharks (Coleman and Holiday 1982). The results of the stomach content survey on three species of sharks, of about 130 specimens examined, collected from the southeast coast of Australia show a surprisingly large component of octopus, 30-60 percent of the total. The rest of the stomach content comprised fish, crustacea, squid, other cephalopods and others. The abundance of octopus, though the species composition is not known, along the southeast Australian coast, is assumed to be substantial. The potential harvest of octopus from the entire area must, therefore, be large enough to support intensive commercial fishing on them.

It is assumed, very roughly, that the potential of total cephalopods in the waters around Australia would be quite large, at least an order of magnitude of the current catch.

3.2.6 Bay of Bengal

The countries bordering the Bay of Bengal as defined in this paper are Thailand (west coast), Burma, Bangladesh and India (east coast). Sri Lanka is included in the eastern Arabian Sea which will be discussed in the next sub-section. Utilization of cephalopod resources have been generally slight with the exception of Thailand where the catch of cuttlefish and squid shows a steady increase since the mid-1970s (Table 9). Although there are no catch statistics for Burma and Bangladesh, the fishing on cephalopods in these two countries is assumed to be extremely low and the current catches may be negligible, judging from the general situation of the fishery in these countries. Even in Thailand substantial fishing was commenced only in 1973 with about a 300 t catch.

Table 9

Catch of cephalopods by species group and country in the Bay of Bengal, including the Andaman Sea
('000 t)

Species group Country	1970	1975	1976	1977	1978	1979	1980	1981
Cuttlefish								
Thailand	–	0	0	4	4	4	3	3
Burma	?	?	?	?	?	?	?	?
Bangladesh	?	?	?	?	?	?	?	?
India[a]	0	2	1	1	1	1	1	1
(Sub-Total)	(0)	(2)	(1)	(5)	(4)	(5)	(4)	(4)
Squid								
Thailand	–	1	1	5	5	5	4	3
Burma	?	?	?	?	?	?	?	?
Bangladesh	?	?	?	?	?	?	?	?
India[a]	0	2	1	1	1	1	1	1
(Sub-Total)	(0)	(2)	(2)	(6)	(6)	(6)	(5)	(5)
Octopus								
Thailand	–	0	0	0	0	0	0	0
Burma	?	?	?	?	?	?	?	?
Bangladesh	?	?	?	?	?	?	?	?
India	?	?	?	?	?	?	?	?
(Sub-Total)	(?)	(0)	(0)	(0)	(0)	(0)	(0)	(0)
Total cephalopods	1	4	3	11	10	12	9	9

[a] Estimated by the author from the figures given by Silas *et al.* (1983), see text

In Thailand most of the catch of cuttlefish and squid (90-95 percent for each species group) have been taken by the trawlers of large-scale fishery and only a small portion has been taken by small-scale fisheries such as push-net and set-bag-net (SEAFDEC 1980, 1981, 1982).

The trawl catch also accounts for the largest component along the east coast of India with 50-60 percent of the total, and the rest is shared by non-mechanized small-scale fisheries such as shore-seines with about 25 percent, boat-seines with about 15 percent, hook and line with about 3 percent and fixed-bag-net with about 1 percent (Silas *et al.*, 1982).

Cuttlefish and Neritic Squid

Species included in the cuttlefish catch are *Sepia pharaonis*, *S. aculeata*, *S. latimanus*, *S. kobiensis* and *Sepiella inermis* (Okutani 1980, Silas *et al.*, 1982) but the proportion of each species is not known. Other species probably occurring in the catches are *S. recurvirostra*, *S. esculenta* and *S. prashadi* (Table 2). There is no doubt on the distribution of some Sepiolidae species in the shallower part of the area but no information has been obtained so far.

Species in the squid catch are *Loligo chinensis*, *L. duvaucelii* and *L. edulis* in larger quantities and *L. singhalensis*, *Sepioteuthis lessoniana* and *Nototodarus philippinensis* probably in smaller quantities (Okutani 1980, Silas *et al.*, 1982). Chotiyaputta (1982) reported *L. uyii* to be distributed in Thai waters but this needs further confirmation. It is interesting to see the successful result of exploratory light-lured jigging of *L. chinensis* in Thai waters where no such fishing has been attempted so far (Shibata, Masthawee and Kitagawa 1980a, Shibata and Masthawee 1980b).

The results of the experimental trawl surveys carried out by the research vessel DR FRIDTJOF NANSEN indicate that the catch rate of cephalopods (presumably mainly cuttlefish) was high along the Thai coast with 2-4 percent of the total catch (Aglen *et al.*,1981) but was lower along the Burmese coast, 0.5-1.9 percent (Strømme *et al.*, 1981), Bangladesh coast, 0.5-2.0 percent (Saetre 1981). A similar trend, i.e., high in the south and low in the north, is also observed on the cephalopod landings along the east coast of India (Silas *et al.*, 1982). These reports suggest that the abundance of cephalopods, especially cuttlefish, in the northern part of the Bay of Bengal, is smaller than in the south. This may also be one of the reasons why so little attention has been paid to cephalopods in the overall review of the fisheries and resources made so far (West 1973, Karim 1978). The potential harvest from the sub-area is assumed, therefore, to be the least among the areas in the Indo-Pacific region, perhaps 5-10 time the current catch on a conservative basis. Chotiyaputta (1982) estimated that the catch of squid along the Thai coast reached the MSY level (about 5 800 t) around 1978. However, the estimate appears to be too small as the estimated MSY refers only to those of demersal type (trawlable) squids excluding pelagic stocks. The resources in the entire sub-area appear, therefore, not to have been fully exploited even in recent years.

Oceanic Squid

The feasibility of the exploitation of oceanic squid in the area is not clear, presumably very low, although a few species are distributed in the southern and open sea area of the Bay as is shown in Table 2 (Filippova 1968).

Octopus

Four species of octopus have been reported from the east coast of India (Voss 1973), and it is assumed that they are distributed commonly along the west coast of the Bay (Jones 1970). No definite information is available for the rest of the Bay, but presumably the distribution is similar to that along the west coast. Octopus resources are virtually not utilized at all in the area.

3.2.7 Eastern Arabian Sea

Although the information on cephalopods in this sub-area is very sparse and fragmentary, there is an indication that abundant resources exist. The bordering countries in the area are Sri Lanka and India (west coast) but catch statistics from Sri Lanka are not available. In addition to the coastal fisheries, the Taiwanese long-range trawl fleet has been operating in the area since 1977 and a substantial amount of cephalopods have been taken (Table 10).

Fisheries

Details of the Sri Lankan fishery are not known. It is said that the fishermen had little interest in catching cephalopod until 1973 when it was realized by fishermen that a good profit could be gained by exporting cephalopod products. Dayaratne (1978) reported that most of the cephalopod catch has been taken as one of by-catch of finfish and shrimps by various types of gears in the waters around Sri Lanka and no aimed fishing has been performed. He also reported that the catch of cuttlefish by trawlers on the Wadge Bank, which is located off the southern tip of India, is the most prominent among the Sri Lanka fisheries with about 20 and 60 t annual catch (during 1970-74) accounting for about 35 percent of the total cuttlefish catch which accounts for approximately 17 percent of the total cephalopod production in Sri Lanka. It is estimated, on the basis of the above, that the total catches of cuttlefish and squid by the Sri Lanka fishery would be about 60-170 t and 280-840 t respectively, resulting in about 340-1 000 t of total annual cephalopod catch during the first half of the 1970s which shows clearly the state of underexploitation of these resources there. No attention appears to have been paid to catching octopus in Sri Lanka.

Table 10

Catch of cephalopods by species group and country in the Eastern Arabian Sea, including waters around Sri Lanka, west coast of India and Laccadive Islands
('000 t)

Species group Country	1970	1975	1976	1977	1978	1979	1980	1981
Cuttlefish								
Sri Lanka	?	?	?	?	?	?	?	?
India[a]	0	2	3	4	7	6	5	6
Taiwan[b]	–	–	–	?	3	0	2[c]	2[c]
(Sub-Total)	(0)	(2)	(3)	(4)	(11)	(7)	(6)	(7)
Squid								
Sri Lanka	?	?	?	?	?	?	?	?
India[a]	0	2	3	4	7	6	5	6
Taiwan[b]	–	–	–	?	1	2	1[c]	1[c]
(Sub-Total)	(0)	(2)	(3)	(4)	(8)	(8)	(6)	(7)
Octopus								
Sri Lanka	?	?	?	?	?	?	?	?
India	?	?	?	?	?	?	?	?
Taiwan[b]	–	–	–	?	0	0	0[c]	0[c]
(Sub-Total)	(?)	(?)	(?)	(?)	(0)	(0)	(0)	(0)
Total cephalopods	0	5	6	8	19	15	12	14

[a] Estimated by the author from the figures given by Silas *et al.* (1982), see text

[b] Long-range pair trawl fleet

[c] Estimated by the author, average during 1978-79

The cephalopod production in India has also experienced a similar process some time in advance (Silas *et al.*, 1982). The catch of cephalopods along the west coast of India was extremely small at 100-400 t until the mid-1960s and steadily increased thereafter. It made great strides especially during the mid-1970s and has been about 12 000-14 000 t in recent years which accounts for about 80-90 percent of the total Indian cephalopod catch including that from the east coast (Table 10). Unfortunately the catch statistics by species group are not available. The author roughly divided the total cephalopod catch into cuttlefish and squid with 50% for each and are given in Table 10. This development has been greatly stimulated by interest in the exportation of products to earn foreign exchange (Silas *et al.*, 1982, Jhingran 1982). The amount in exports has been increasing steadily in recent years (Hotta 1982a). The bulk of the catch has been achieved by trawlers; about 60 percent, followed by hook and line: 17 percent; shore-seines: 10 percent; boat seines: 10 percent and stake-nets: 4 percent (Silas *et al.*, 1982). The fishing grounds of these fisheries are limited to the shallower part of the shelf, down to 40 m depth. It is believed, therefore, that the Indian fishery utilizes only a part of the cuttlefish and squid resources. Although octopus resources are reported to be distributed widely along the west coast of India, no substantial commercial fishing has been performed due probably to the unpopularity of octopus in Indian food, and the utilization of octopus only as bait for longline fishermen has been reported (Jones 1970).

The long-range trawl fleet of Taiwan, Province of China, operate in the waters around Sri Lanka and along the west coast of India extending to the eastern Pakistani waters and a substantial amount of cuttlefish and squid have been caught (Table 10) (DFRCT 1979, 1980).

Information on the species composition of the catch is not available for any of the above-mentioned fisheries. The probable composition of the major species is reviewed, therefore, mostly from the academic reports and are summarized as shown in Table 2.

Cuttlefish and Neritic Squid

Among the cuttlefishes, *Sepia pharaonis* and *S. prashadi* may be taken in larger quantities, followed by *S. lycidas*, *S. kobiensis* and *Sepiella inermis* (Okutani 1980, Silas *et al.*, 1982, Perera 1975, Dayaratne 1978). Probably the other species are *S. recurvirostra*, *S. latimanus* and *S. esculenta*, and some species of Sepiolidae may also be abundantly distributed in the shallower part of the area. However, these assumptions need future confirmation.

Among squids, *Loligo duvaucelii* and *Sepioteuthis lessoniana* appear to be most abundant followed by *L. edulis*, *L. singhalensis* and *Nototodarus philippiensis* (Okutani 1980, Silas *et al.*, 1982, Perera 1975). It is somewhat strange that *L. chinensis* has not been reported from the area as the species is commonly distributed in tropical areas in the region including neighbouring waters in the eastern part of the Bay of Bengal (Shibata, Masthawee and Kitagawa 1980a, Shibata and Masthawee 1980b). The author assumes that *L. chinensis* may also be distributed in the area but this needs future confirmation.

The results of a number of surveys carried out by various institutions gives positive proof that cuttlefish and squid exist abundantly in the area. A series of exploratory purse-seining surveys at night with luring light in the waters around Sri Lanka, which was originally aimed at the bait fish survey for pole and line skipjack fishing caught a substantial amount of squid, 1-6 percent of the total catch (Joseph 1974, 1975). The size of squid ranged widely, 6-23 cm ML but the species were not identified (Joseph 1974). It was possibly a mixture of several species. Experimental bottom trawling and pelagic trawling carried out by the research vessel DR FRIDTJOF NANSEN around Sri Lankan waters frequently caught cuttlefish/squid (not separated) in substantial amounts, ranked at second to fifth among the species caught (Saetersdal and de Bruin 1978; Blindheim, de Bruin and Saetersdal 1979; Blindheim and Føyn 1980). A Japanese research vessel SHOYO MARU caught *L. duvaucelii* in substantial quantities by jigging with light at night during her two cruises in two successive years (Yamanaka, Nishikawa and Morita 1976; Yamanaka, Yukinawa and Nakamura 1977). It should also be noted here that the Indian fisheries have been catching some amounts of cephalopods consistently from the waters around the Loccadive Islands where an oceanic regime rules (Silas *et al.*, 1982). All this information supports the assumption that there is an abundant distribution of pelagic form of cuttlefish/squid in the area.

By putting together all the information the potential harvest of cuttlefish and squid from the entire sub-area is estimated to be quite large roughly about 10 fold of the present catch.

Oceanic Squid

There have been a number of records which confirm the abundant and wide distribution of several oceanic squid species (Table 2). *Symplectoteuthis oualaniensis* appear to be the most abundant and were reported from both the coastal and offshore-oceanic waters (Silas 1969; Filippova 1968; Yamanaka, Nishikawa and Morita 1976; Yamanaka, Yukinawa and Nakamura 1977). The fishing methods applied were drift gillnet at night by Indian research vessels (Silas 1969), round dipnet and pelagic trawl at night with light attraction by the USSR research vessels (Filippova 1968) and jigging both in daytime without light and at night with light attraction by Japanese research vessels (Yamanaka, Nishikawa and Morita 1976; Yamanaka, Yukinawa and Nakamura 1977). It is interesting to see that squid were caught even in the daytime (16.30-17.20 h) without light attraction, while the species generally appeared to inhabit the 120-200 m depth zone during the daytime judging from the acoustic data. However, once a few squid were jigged at the deep layer by a longline hook and hauled on board, many specimens were attracted towards the surface and jigged at the near-surface layer (Yamanaka, Nishikawa and Morita 1976). There is no doubt, therefore, on the abundant distribution of *S. oualaniensis* in the area. However, further surveys are required both on biology and oceanographic conditions to ascertain the feasibility of commercial fishing, particularly in connection with the formation of the fishing ground with a dense school.

Onychoteuthis banksii and *Thysanoteuthis rhombus* are also distributed in the area but probably in smaller abundance (Filippova 1968). The possibility of commercial fishing on these species is not known, but it is said that they do not usually form a large or dense school (Okutani 1980).

Octopus

Four species of octopus have been confirmed in the sub-area (Table 2). Almost no commercial fishing has been employed in the area as was described in the earlier part of this sub-section. Substantial amount of the octopus could possibly be harvested from the area if suitable fishing methods are introduced.

4. DISCUSSIONS

4.1 Neritic Cephalopods

The majority of the stocks of cuttlefish, neritic squid and octopus in the region have been only slightly exploited so far with the exception of a few local stocks. Although cuttlefish in the East China Sea to the Formosa Strait, cuttlefish and squid around Hong Kong and in the Gulf of Thailand and Malacca Strait, appear to have been more or less intensively exploited, those which inhabit non-trawlable waters and the pelagic form of squid seem to have remained almost untapped even in these areas, with the exception of the very limited waters around Hong Kong. It is believed therefore that the exploitable potential of cuttlefish and neritic squid from the entire region is at a far higher level than that of the current catch.

It is also noted that octopus resources have been virtually unexploited in many areas in the region. Even in the Gulf of Thailand, where a substantial part of the catch has been taken by Thai trawlers, many unutilized stocks seem to be distributed along rocky or gravelly coasts. The biomass and potential yield of octopus generally appear not to be so large as those of cuttlefish or squid. However, a substantial amount can undoubtedly be harvested. For instance, in Japan and Italy, where intensive octopus fishing has been carried out by aimed fishing with traps and hook and lines, the catch of octopus usually accounts for 10-15% (or 50 000-70 000 t) of total cephalopod catch in Japan and 25-35% (or 10 000-20 000 t) in Italy. It is believed therefore that the potential harvest of octopus is substantial and a greatly increased production could be achieved in many areas in the region if a suitable aimed fishing method is introduced. An example on successful exploratory fishing by traps in Australian waters supports this assumption. No explicit estimate of potential yield has been made so far for any stocks of cephalopods in the Indo-Pacific region with the exception of Japanese flying squid in waters around Japan. The author roughly estimated the potential yield of neritic cephalopods by sub-area employed in this review. The estimation was made on a conservative basis, being based on the findings obtained through the review study presented in this paper. The estimates in comparison with the current catch are given in Table 11.

In total, about 1.05-1.40 million tons of neritic cephalopods could be harvested from the Indo-Pacific region defined in this paper, which is about 3-5 times the current catch. The largest increase in the catch could be obtained from the Indonesian and Australian waters where local commercial fisheries have been very inactive in spite of what appears to be large potential yields. The Bay of Bengal, although the local fisheries are very inactive, may have the lowest potential yield among the areas. The waters around the Philippines and the eastern Arabian Sea may also have a lot of scope for increased exploitation. The South China Sea and the Yellow Sea-East China Sea, where relatively intensive exploitation has been undertaken, still seem to retain some opportunities for future expansion. However, in these two sub-areas potential for future expansion may be somewhat less than in the other areas in terms of the species caught (fishing methods) and the fishing ground to be expanded.

If similar estimates for the northern Northwest Pacific and the waters around New Zealand are included, although the estimate for the latter is rather arbitrary, the total potential from the so-called Indo-Pacific region defined by FAO comes out to be around 1.7-2.2 million tons of which about half has been currently utilized (Table 11).

Table 11

Estimated potential yield of neritic cephalopods by sub-area in the Indo-Pacific region in comparison with the current catch ('000 t)

Sub-Area	Average catch 1979-81	Estimated potential	Catch/potential
Yellow Sea and East China Sea	119	200 - 250	0.60-0.48
Waters around Philippines	31	100 - 150	0.31-0.21
South China Sea	96	200 - 250	0.47-0.38
Java Sea to northern Arafura Sea	13	200 - 250	0.07-0.05
Waters around Australia	14	200 - 250	0.07-0.06
Bay of Bengal	10	50 - 100	0.20-0.10
Eastern Arabian Sea	14	100 - 150	0.14-0.09
Total region	296	1 050-1 400	0.28-0.21
Northern Northwest Pacific	649	500 - 600[a]	Fully exploited[a]
Waters around New Zealand	63	100 - 150[b]	Unknown[a], 0.63-0.42[b]
(Sub-Total)	(712)	(600 - 750)	(1.00-0.95)
Total[c]	1 008	1 650-2 150	0.61-0.47

[a] After FAO (1981)

[b] Estimated by the author, rather arbitrary

[c] Entire area is nearly equivalent to the so-called "Indo-Pacific Region" defined by FAO

Voss (1973) estimated the potential yield of neritic cephalopods (continental shelf fisheries) by the major FAO fishing areas. It appears that his estimate is too large for the Northwest Pacific (2-3 times that of the author) but is reasonable and very close to the author's (close to the lower margin or fall in the range) for the other areas.

The above estimated potential of 1.1-1.4 million tons in the region is considerably greater than the current catch of 0.3 million tons. However, strategic problems may well arise if the cephalopod fisheries are to be further developed. Firstly, it is well known that many demersal fish stocks have already been heavily fished in many areas in the region and therefore the general intensification of trawl fishing is not advisable. Secondly, trawling is obviously inapplicable for pelagic forms of cephalopods or those which inhabit rocky bottoms. Other fishing methods such as jigging, hook and line, traps, fixed set-net and seining are therefore needed in many nations to develop the cephalopod fishery. It is not likely however that modern mechanized jigging by powerful lights and machines (as used in Japan) is applicable to the many countries where small-scale fisheries compose the majority of coastal fisheries. The large-scale fishing by traps for cuttlefish and octopus may also involve some difficulties, such as installations of mechanized line-haulers, etc. The rational utilization of neritic cephalopods in the region will not therefore be achieved until a well-balanced strategy is established to overcome these problems.

Another strategic or socio-economic problem is the question of how local fishermen would be interested in fishing neritic cephalopods. As was described in the introductory part of this paper many countries have began to pay more attention to exporting cephalopod products in order to earn foreign exchange. This has probably increased profitability, and encouraged the fishermen to engage more in catching cephalopods, as seems to be the case in India (Table 10, 12), but exportation of cephalopods is still minor or stagnant in many countries (Table 12). There may be some limiting factors for local fisheries for producing export material especially for small-scale fishermen. These may include problems of handling and preservation facilities on board, the landing and processing (freezing) facilities on land and the domestic network for transporting the products/catch to the shipping site.

There may also be some risk that the demand is far from unlimited. So far, the quantity of cephalopod products (mostly frozen) imported by major importing countries, appears to keep growing (Table 13). However, this growth cannot be indefinite and the quantity imported is generally closely linked with changes in the local production in the importing countries. For instance, the sudden and large decrease in the imports by Japan in 1980 was caused mainly by the good fishing for Japanese flying squid around Japan in that year.

The better development strategy might therefore be to concentrate first on increasing domestic consumption. Otherwise, the introduction of new fishing methods for catching cephalopods could impose some risky venture on local fishermen which might hamper in the long-term effective and rational utilization of the large potential yield of neritic cephalopods.

4.2 Oceanic Squid

There have been fairly positive indications on the possibility of commercial fishing for a few oceanic squid in several areas in the region. The most promising evidence were for the exploitation of *Ommastrephes bartrami* in the southeastern waters of Australia and *Symplectoteuthis oualaniensis* in the eastern Arabian Sea, and in the western Pacific Ocean to the eastward of the Philippines and Indonesia. However, it is premature to say much about the feasibility of commercial fishing for these squid at this stage with the exception of the existing fisheries in the western Pacific Ocean. The availability of these species in terms of likely catch rates for local fisheries is still unknown even though the potential yield is believed to be large.

5. RECOMMENDATIONS ON FUTURE STUDIES

As has been described in the previous sub-sections, information on the biology and commercial catch of cephalopods is very sparse and fragmentary which makes the assessment of resources extremely difficult. It is impracticable to improve the situation at once in many fields simultaneously. However, the surveys and studies on a few essential fields should be urgently carried out. These fields and the major lines to be achieved are summarized as follows.

5.1 Neritic Cephalopods

Only a few species of cuttlefish and squid in limited areas have been studied (Chotiyaputta 1982, Silas *et al.*, 1982) and almost nothing has been done for octopus.

(1) Species identification

This is the most important problem which involves two types of questions. One is to identify the major species occurring in each of the areas where no substantial study has been carried out and the other is the further clarification of species or sub-species for some specific species where there are substantive doubts. The first question is essential generally in all the areas concerned but specifically in Indonesian and Australian waters and in the eastern Indian Ocean. The second question is relevant for *Loligo edulis* in many areas.

(2) Distribution, range and stock identity

A direct approach to this question may be difficult. The accumulation of as many observations as possible on the species, species composition and size frequency distribution of the catch should be planned. The data should then be analysed with the aid of the information on spawning and other biological information.

Table 12

Export of cephalopod products by each of the countries in the Indo-Pacific region during 1976-80[a]
('000 t)

Country	1976	1977	1978	1979	1980
China	5	2	3	4	3
Taiwan, Province of China	0	5	9	8	6
Hong Kong	3	2	2	2	2
Philippines	0	1	1	1	?
Thailand	22	35	45	49	44
Viet Nam	-	-	-	-	-
Kampuchea	-	-	-	-	-
Malaysia	1	2	?	?	?
Singapore	-	-	-	1	1
Indonesia	-	-	-	-	-
Australia[b]	-	-	-	-	-
Burma	-	-	-	-	-
Bangladesh	-	-	-	-	-
India	1	2	3	3	4
Sri Lanka[b]	-	-	-	-	-
Total	32	49	63	68	60

a/ Source: Hotta (1982a)

b/ Very small amount is probably exported in recent years

Table 13

Import of cephalopod products by major importing countries in the world during 1976-80[a]
('000 t)

Country	1976	1977	1978	1979	1980
Japan	174	147	205	226	167
Italy	33	29	43	46	43
Spain	34	25	43	42	48
Taiwan, Province of China	1	3	9	14	18
France	8	7	10	12	11
Greece	8	7	11	9	10[b]
Total	258	218	321	349	297
World Total	268	230	332	370	304

a/ Source: Hotta (1982a)

b/ Estimated by the author, average of 1978-79

(3) Spawning season and ground

This is also most important information which is urgently required. Information or sample specimens could be collected from commercial fisheries in the area where substantial commercial fishing is performed but special surveys by research vessels are needed in other areas.

(4) Biological features of each species

Studies on many biological features specifically on habitat, migration, diurnal changes in behaviour, growth, length-weight relationship and feeding, should be carried out.

(5) Oceanographic and environmental condition

Oceanographic surveys have been in the past or will be in the future undertaken by many institutions for various purposes. The data from these surveys need to be examined in connection with the ecological/biological requirements of cephalopods. Special observations may be needed in monsoon areas.

(6) Regional collaboration

This is extremely important to approach effectively the appraisal of cephalopod resources for two reasons:

(a) many stocks may migrate through the waters of two or more national jurisdictions

(b) there must be large local variations on behaviour and biological features of the same species for which comparative studies would be the most effective.

(7) Experimental fishing with new methods

This should be carried out to assist future development of cephalopod fisheries which need not depend on large-scale modernization or mechanization but should be aimed at the introduction of locally suitable fishing methods and at the adaptation of indigenous fisheries to them.

(8) Catch and effort data collection

In addition to the improvement of the data collection from trawl fisheries, which is likely to remain the major fishing method for the time being, the catch and effort data from the newly expanded/employed fisheries should be intensively collected as the trawl data may give information on only one segment of the resources.

5.2 Oceanic Squid

Conventional resources survey methods seem to be inapplicable to these stocks and may not be relevant in the region for the time being as the potential yield is probably extremely large and the fishing mortality may be a minor factor on population dynamics of these stocks. The feasibility study on commercial fishing may therefore be the major lines in which to be engaged. Exploratory fishing by jigging and drift gillnet appears to be the most suitable approach for development. The biological study on the specimens collected by these explorations should, needless to say, give us valuable information to establish commercial fishing on these stocks.

Collaboration on a regional and interregional basis should be maintained as the survey on the important items of these stocks, such as distribution, spawning and environment, cannot be covered by any coastal countries alone.

6. REFERENCES

Aglen, A. et al., 1981 A survey of the marine fish resources of the west coast of Thailand, July 1980. Reports on surveys with the R/V DR. FRIDTJOF NANSEN. Bergen, Institute of Marine Research, 55 p.

Aoki, J. et al., 1965 Cephalopods. In Illustrated encyclopaedia of the fauna of Japan, edited by K. Okada, et al. Tokyo, Hokuryu-kan, Vol.2:307-26

Beck, U. and A. Sudradjat, 1978 Variations in size and composition of demersal trawl catches from the north coast of Java with estimated growth parameters for three important food-fish species. Special report. Contrib.Demersal Fish.Proj.Mar.Fish.Res.Inst.,Jakarta, (4):80 p.

Blindheim, J., G.H.P. de Bruin and G. Saetersdal, 1979 A survey of the coastal fish resources of Sri Lanka, Report no. 2, April-June 1979. Reports on surveys with the R/V DR. FRIDTJOF NANSEN. Bergen, Institute of Marine Research, 63 p.

Blindheim, J. and L. Føyn, 1980 A survey of the coastal fish resources of Sri Lanka, Report no. 3, January-February 1980. Reports on surveys with R/V DR. FRIDTJOF NANSEN. Bergen, Institute of Marine Research, 78 p.

Buzeta, R.B., A. Dwiponggo and T. Sujastani, (eds.), 1979 Report of the workshop on demersal and pelagic fish resources of the Java Sea. Semarang, Indonesia, 5-9 December 1978. Manila, South China Sea Fisheries Development and Coordinating Programme, SCS/GEN/79/20:60 p.

Chen, S., 1982 Effect of typhoons on the catch of cuttlefish in the East China Sea. Ocean Fish., 4(1):7-8 (in Chinese)

Chotiyaputta, C., 1982 Squid fisheries of Thailand. FAO Fish.Rep., (275):124-7

Coleman, N. and D. Holiday, 1982 Squid not vital in the diets of commercially-important fish from SE Australia. Aust.Fish., 41(11):6-8

Collins, S. and M. Dunning, 1981 Tasman squid studies demonstrate gillnetting effective. Aust.Fish., 40(8):2, 4-6

Davidson, A., 1976 Seafood of southeast Asia. Singapore, Federal Publications Pte Ltd., 366 p.

Dayaratne, N.M.P.J., 1978 A preliminary study on the cuttlefish catches from the Wadge Bank trawl fishery. Bull.Fish.Res.Stn., Sri Lanka, (28):27-35

Demersal Fish Research Center of Taiwan, 1972 Annual report of effort and catch statistics by area on Taiwan demersal fish fisheries, 1971. Annu.Rep.Effort Catch Stat.Area Taiwan Demersal Fish Fish., (1971):94 p.

__________, 1976 Annual report of effort and catch statistics by area on Taiwan demersal fish fisheries, 1975. Annu.Rep.Effort Catch Stat.Area Taiwan Demersal Fish Fish., (1975):227 p.

__________, 1977 Annual report of effort and catch statistics by area on Taiwan demersal fish fisheries, 1976. Annu.Rep.Effort Catch Stat.Area Taiwan Demersal Fish Fish., (1976):195 p.

———, Annual report of effort and catch statistics by area on Taiwan
1978 demersal fish fisheries, 1977. Annu.Rep.Effort Catch Stat.Area Taiwan Demersal Fish Fish., (1977):157 p.

———, Annual report of effort and catch statistics by area on Taiwan
1979 demersal fish fisheries, 1978. Annu.Rep.Effort Catch Stat.Area Taiwan Demersal Fish Fish., (1978):216 p.

———, Annual report of effort and catch statistics by area on Taiwan
1980 demersal fish fisheries, 1979. Annu.Rep.Effort Catch Stat.Area Taiwan Demersal Fish Fish., (1979):237 p.

Dong, Z., The present status and the prospects of cephalopod resources in the
1981 west Pacific. J.Fish.China, 5(3):263-70

Dong, Z., et al., Cephalopod larvae from the northern South China Sea.
1981 Oceanol.Limnol.Sin., 12(5):457-62

Dunning, M., Squid and cuttlefish resources of Australian waters. FAO
1982 Fish.Rep., (275):103-8

Dwiponggo, A. and M. Badrudin, Results on the Java Sea inshore monitoring
1980 surveys, 1979. Special report. Contrib.Demersal Fish.Proj.Mar. Fish.Res.Inst.,Jakarta, (7):109 p.

FAO., Contributed papers submitted to the expert consultation on fishing for
1976 squid and other cephalopods. Tokyo and Hakodate, Japan, 9-13 September 1975. Supplement to the Report. FAO Fish.Rep., (170) Suppl.1:150 p. Issued also in French and Spanish

———, Review of the state of world fishery resources. FAO Fish.Circ.,
1981 (710) Rev.2:52 p. Issued also in French, Spanish, Arabic and Chinese

Filippova, J.A., New data on the Cephalopoda of the Indian Ocean.
1968 Symp.Ser.Mar.Biol.Assoc.India, 3(Pt.1):257-64

Hernando, A.M. and E.C. Flores, The Philippines squid fishery: a review.
1981 Mar.Fish.Rev., 43(1):13-20

Hotta, M., The Japanese market for squid and cuttlefish. INFOFISH Marketing
1982 Dig., (4):12-9

———, International market for cephalopods. Kuala Lumpur, INFO-
1982a FISH, (ADB/FAO/INFOFISH), 53 p.

Indo-Pacific Fishery Commission (IPFC), Report of the third session of the
1982 standing committee on resources research and development. Sydney,Australia,28 April-4 May 1982. FAO Fish. Rep., (275):135 p.

Ishii, M., Studies on the growth and age of the squid, Ommastrephes bartrami in
1977 the Pacific off Japan. Bull.Hokkaido Reg. Fish Res.Lab., (42):25-36

Itami, K., Seto Inland Sea type octopus fishery in connection with the develop-
1975 ment of octopus farming technique. In Exploitation and utilization of cephalopod resources in the world. Inf.Doc.Jap.Mar.Fish. Resour.Res.Cent.,Tokyo, (5):179-84 (in Japanese)

Japan Marine Fishery Resource Research Center, Report of feasibility study on
1978 squid jigging fisheries in the southwestern Pacific Ocean, 1977. JAMARC Rep., (18):163 p.

———, Report of feasibility study on squid jigging fisheries in the
1980 southwestern Pacific Ocean, 1978. JAMARC Rep., (19):178 p.

Jhingran, V.G., Fish and fisheries of India. Delhi, Hindustan Publishing Corporation
1982 (India), 666 p. Rev. enlarged 2nd ed.

Jones, S., The molluscan fishery resources of India. *Symp.Ser.Mar.Biol.Assoc.*
1970 *India*, 3(Pt.3):906-18

Joseph, B.D.L., Preliminary report on experimental fishing with purse-seine and
1974 lampara nets for small pelagic fish varieties around Sri Lanka. *Bull.Fish.Res.Stn.Sri Lanka*, 25(1-2):1-13

____________, Purse seining for small pelagic fish around Sri Lanka. *Bull.Fish.*
1975 *Res.Stn.Sri Lanka*, 26(1-2):31-43

Karim, M., Status and potential of Bangladesh fisheries. Dacca, Bangladesh,
1978 Ministry of Fisheries and Livestock, 126 p.

Kawakami, T., The fishery biological study on a squid, *Nototodarus sloani sloani*
1976 (Gray), in the New Zealand waters. *Bull.Tokai Reg.Fish.Res.Lab.*, (85):31-104

Kawakami, T. and T. Okutani, A note on identity of Ommastrephid squids of the
1981 Genus *Nototodarus* exploited in the New Zealand waters. *Bull.Tokai Reg.Fish.Res.Lab.*, (105):17-30

Latif, M.S.B.S.A., Malaysian squid resources. *FAO Fish.Rep.*, (275):118-20
1982

Li, X. and J. Dai, Consideration on artificial breeding of a cuttlefish, *Sepiella*
1982 *japonica*, for propagation purpose. *Ocean Fish.*, 4(1):2-6 (in Chinese)

Liu, H.C., H.L. Lai and S.Y. Yeh, General review of demersal fish resources in
1978 the Sunda Shelf and the Australian waters. *Acta. Oceanogr. Taiwan*, (8):109-40

Liu, H.C. and C.L. Kao, General review of demersal resources around Taiwan.
1979 *Acta Oceanogr.Taiwan.*, (9):77-96

Losse, G.F. and A. Dwiponggo, Report on the Java Sea southeast monsoon trawl
1977 survey, June-December 1977. Special report. *Contrib.Demersal Fish.Proj.Mar.Fish.Res.Inst.,Jakarta*, (3):93 p.

Martosubroto, P. and D. Pauly, R/V MUTIARA IV survey data, November 1974
1976 to July 1976. Special report. *Contrib.Demersal Fish.Proj.Mar.Fish.Res.Inst.,Jakarta*, (2):136 p.

Mattlin, R.H., New Zealand squid fishery. *FAO Fish.Rep.*, (275):120-3
1982

Murata, M., M. Ishii and H. Araya, The distribution of the oceanic squids,
1976 *Ommastrephes bartrami*, *Onychoteuthis borealijaponica*, *Gonatopsis borealis* and *Todarodes pacificus* in the Pacific Ocean off northern Japan. *Bull.Hokkaido Reg.Fish.Res.Lab.*, (41):1-29

Murata, M. and T. Ishii, Some information on the ecology of the oceanic squid,
1977 *Ommastrephes bartrami* (Lesuer) and *Onychoteuthis borealijaponica* Okada, in the Pacific Ocean off northern Japan. *Bull.Hokkaido Reg.Fish.Res.Lab.*, (42):1-25

Murata, M. and Y. Shimazu, On some population parameters of flying squid
1982 *Ommastrephes bartrami* (Lesuer) in the Northwest Pacific. *Bull.Hokkaido Reg.Fish.Res.Lab.*, (47):1-10

National Federation of Fisheries Cooperative Association of Japan, A report on
1979 the feasibility fishing for squid by 8 Japanese vessels in the Tasmanian waters for the 1978/79 fishing season. Tokyo, National Federation of Fisheries Cooperative Association of Japan, 9 p., 4 tables, 10 figures, 3 appendix tables and 14 appendix figures (mimeo)

Okutani, T., Stock assessment of cephalopod resources fished by Japan. FAO
1977 Fish.Tech.Pap., (173):62 p.

________, Useful and latent cuttlefish and squids of the world. Tokyo,
1980 National Cooperative Association of Squid Processors, 66 p.

Okutani, T. and I.H. Tung, Reviews of biology of commercially important squids
1978 in Japanese and adjacent waters, I. Symplectoteuthis oualaniensis (Lesson). Veliger, 21(1):87-94

Pauly, D., Theory and management of tropical multispecies stocks; a review on
1979 the Southeast Asian demersal fisheries. ICLARM Stud.Rev., (1):1-35

Perera, N.M.P.J., Taxonomic study of the cephalopods, particularly the
1975 Teuthoidea (squids) and Sepioidea (cuttlefish) in the waters around Sri Lanka. Bull.Fish.Res.Stn.Sri Lanka. 26(1-2):45-60

Ritragsa, S., Results of the studies on the status of demersal fish resources in
1976 the Gulf of Thailand from trawling surveys, 1963-1972. In Proceedings of the Seminar on fisheries resources and their management in Southeast Asia, edited by K. Tiews. Organized by the German Foundation for International Development, the Federal Research Board for Fisheries, and FAO. Bonn, Druckerei Heinz Lammerich. pp.198-223

Roberts, P.E., New Zealand squid resources. Occas.Publ.Fish.Res.Div.N.Z.,
1978 (15):90-3

Roper, C.F.E. and R.E. Young, Vertical distribution of pelagic cephalopods.
1975 Smithsonian Contr.Zool., (209):1-51

Saetersdal, G.S. and G.M.P. de Bruin, Report on a survey of the coastal fish
1978 resources of Sri Lanka, August-September 1978. Reports on surveys with the R/V DR. FRIDTJOF NANSEN. Bergen, Institute of Marine Research, 29 p.

Saetre, R., Surveys on the marine fish resources of Bangladesh, November-
1981 December 1979 and May 1980. Reports on surveys with the R/V DR. FRIDTJOF NANSEN. Bergen, Institute of Marine Research 67 p.

Sakurai, T., Squid and cuttlefish fisheries in Thailand. Proc.IPFC, 15(3):496-511
1974

Shibata, K., P. Masthawee and Y. Kitagawa, A preliminary study on squid fishing
1980a around Phuket waters employing squid handline, a new fishing technique in Thai waters. Curr.Tech.Pap.Ser.Train.Dep., SEAFDEC, (8):14 p.

Shibata, K. and P. Masthawee, Experimental echo survey for squid fishing
1980b around the Phuket waters. Curr.Tech.Pap.Ser.Train.Dep., SEAFDEC, (9):30 p.

Shin, P.K.S., The Hong Kong squid fishery. FAO Fish.Rep., (275):112-4
1982

Silas, E.G., 1968 Cephalopoda of the west coast of India collected during the cruise of the research vessel VARUNA, with a catalogue of the species known from the Indian Ocean. Symp.Ser.Mar.Biol.Assoc.India, 3(Pt.1):277-359

Silas, E.G., 1969 Exploratory fishing by R.V. VARUNA. Bull.Cent.Mar.Fish.Res.Inst., India. (12):1-86

Silas, E.G., 1982 et al., The exploited squid and cuttlefish resources of India. Tech.Ext.Serv.Mar.Fish.Inf.Serv.CMFRI,Cochin, (34):1-17

Simpson, A.C. (ed.), 1978 Report of the BFAR/SCSP Workshop on the fishery resources of the Pacific coast of the Philippines. Naga City, Philippines, 18-22 September 1978. Manila, South China Sea Fisheries Development and Coordinating Programme, SCS/GEN/78/19:48 p.

____________, 1979 Report of the BFAR/SCSP Workshop on the fishery resources of the north and western coast of Luzon. Manila, Philippines, 18-20 April 1979. Manila, South China Sea Fisheries Development and Coordinating Programme, SCS/GEN/79/22:57 p.

Smith, P.J., 1981 P.E. Roberts and R.J. Hurst, Evidence for two species of arrow squid in the New Zealand fishery. New Zealand Jour.Mar.Freshw.Res., 15:247-53

South China Sea Fisheries Development and Coordinating Programme, 1976 Report on the BFAR/SCSP Workshop on the fishery resources of the Visayan and Sibuyan sea. Iloilo, Philippines, 18-22 October 1976. Manila, South China Sea Fisheries Development and Coordinating Programme, SCS/GEN/76/2:85 p.

____________, 1976a Report of the Workshop on the fishery resources of the Malacca Strait. Part 1. Jakarta, Indonesia, 29 March-2 April 1976. Manila, South China Sea Fisheries Development and Coordinating Programme, SCS/GEN/76/7:26 p.

____________, 1976b Report of the Workshop on the fishery resources of the Malacca Strait. Part 2. Jakarta, Indonesia, 29 March-2 April 1976. Manila, South China Sea Fisheries Development and Coordinating Programme, SCS/GEN/76/6:113 p.

____________, 1978 Report of the Workshop on the demersal resources of the Sunda Shelf. Part 1. Penang, Malaysia, 31 October-4 November 1977. Manila, South China Sea Fisheries Development and Coordinating Programme, SCS/GEN/77/12:44 p.

____________, 1978a Report of the Workshop on the demersal resources of the Sunda Shelf. Part 2. Penang, Malaysia, 31 October-4 November 1977. Manila, South China Sea Fisheries Development and Coordinating Programme, SCS/GEN/77/13:120 p.

____________, 1978b Report of the Workshop on management of resources of the Sunda Shelf, Malacca Strait and related areas. Manila, Philippines, 7-9 December 1977. Manila, South China Sea Fisheries Development and Coordinating Programme, SCS/GEN/78/18:15 p.

Southeast Asian Fisheries Development Center, 1980 Fishery statistical bulletin for South China Sea area, 1978. Fish.Stat.Bull.South China Sea Area, (1978):200 p.

————, Fishery statistical bulletin for South China Sea area, 1979.
1981 Fish.Stat.Bull.South China Sea Area, (1979):201 p.

————, Fishery statistical bulletin for South China Sea area, 1980.
1982 Fish.Stat.Bull.South China Sea Area, (1980):227 p.

Strømme, T. et al., Surveys on the marine fish resources of Burma. September-
1981 November 1979 and March-April 1980. Reports on surveys with the R/V DR. FRIDTJOF NANSEN. Bergen, Institute of Marine Research, 89 p.

Tung, I.H., On the biology and the fishing of the squid, Nototodarus sloani sloani
1978 (Gray), in the New Zealand waters. Rep.Inst.Fish.Biol., Taipei, 3(3):44-64

————, A list of decapodous cephalopods in Taiwan.
1978a Rep.Inst.Fish.Biol,Taipei, 3(3):65-7

————, On the fishery and the biology of the squid, Ommastrephes
1981 bartrami, in the northwest Pacific Ocean. Rep.Inst.Fish.Biol., Taipei, 3(4):12-37

Tung, I.H., C.S. Lan and C.C. Hu, The preliminary investigation for exploitation
1973 of common squid resources. Rep.Inst.Fish.Biol.Taipei, 3(1):211-47

Unar, M. and M. Sahabi, A small-scale squid fishery in Alas Strait, West
1982 Nusatenggara. FAO Fish.Rep., (275):116-7

Voss, G.L., Cephalopods of the Philippine Islands. Bull.U.S.Natl.Mus., (234):1-
1963 180

————., Cephalopod resources of the world. FAO Fish.Circ., (149):75 p.
1973

Voss, G.L. and G.R. Williamson, Cephalopods of Hong Kong. Hong Kong,
1971 Government Press, 138 p.

West, W.Q.B., Fishery resources of the upper Bay of Bengal. Rome, FAO,
1973 IOFC/DEV/73/28:44 p.

Yamanaka, H., Y.Nishikawa and J. Morita, Summary report on cruise of the R/V
1976 SHOYO MARU in the north Arabian Sea, 2 October 1975 to 14 January 1976. Tech.Rep.Indian Ocean Programme, (IOP/TECH/76/11):46 p.

Yamanaka, H., M. Yukinawa and I. Nakamura, Summary report on cruise of the
1977 R/V SHOYO MARU in the north Arabian Sea, 2 October 1976 to 13 January 1977. Tech.Rep.Indian Ocean Programme, (IOP/TECH/77/14):82 p.

Yoshikawa, N., Fisheries in Japan : squid and cuttlefish. Tokyo, Japan Marine
1978 Products Photo Materials Association, 161 p.

Yu, K., Preliminary analysis of the decrease in cuttlefish production in the East
1981 China Sea during summer 1981. Ocean Fish., (6):2-3 (in Chinese)

Anon., A possible octopus fishing industry in western Australia. FINS, 13(1):4-6
1980

_____________, Octopus survey. FINS, 13(2):21-2
1980a

_____________, Further support for possible octopus industry. FINS, 14(4):3-6
1981

_____________, Catching squid in Bass Strait. FINS, 15(1):3-6
1982

_____________, West coast exploratory trawl - TAIYO MARU 71. FINS, 15(2):16-
1982a 21

ON THE FISHERY AND BIOLOGY OF THE GIANT SQUID *DOSIDICUS GIGAS* IN THE GULF OF CALIFORNIA, MEXICO

by

Nelson M. Ehrhardt, Pierre S. Jacquemin, Francisco García B.,
Germán González D., Juan Manuel López B., Juan Ortiz C. and Agustín Solís N.

ABSTRACT

The population of giant squid in the Gulf of California is clearly a single stock with multiple cohorts. These migrate separately on occasions but are contemporaneous: their recruitment to the major fishing grounds occurs around May each year. From May to September the stock presents the highest densities and thus an optimum situation for the fishery.

The cohorts grow at different rates depending on their birth date, and probably their natural mortality rates are equally different even though it has been impossible to measure this parameter separately for each cohort as yet.

Stock assessment analyses indicate that after explosive fishery development, the stock is approaching the Maximum Sustainable Yield (MSY). Management schemes are difficult to define unless the fishery is regulated in terms of the less productive cohorts, and since *D. gigas* is a fast growing and fast dying species, it is essential to obtain better knowledge of its reproduction potential before advice in terms of fishing levels can be given.

RESUME

Les populations de calmars géants du golfe de Californie appartiennent manifestement à un stock unique divisé en plusieurs cohortes. Il arrive parfois qu'elles émigrent séparément, mais elles le font en même temps. Elles gagnent généralement les principaux lieux de pêche aux alentours de mai de chaque année. C'est de mai à septembre que le stock présente la plus haute densité, et donc les conditions les plus avantageuses pour la pêche.

Le rythme de croissance des différentes cohortes varie en fonction de la date de naissance, et sans doute le taux de mortalité naturelle varie également, bien que l'on ne soit pas encore parvenu à mesurer ce paramètre séparément pour chaque cohorte.

Il ressort de l'évaluation des stoks qu'après un développement spectaculaire de la pêche, les stocks semblent approcher le niveau du rendement eumétrique. Il paraît difficile d'énoncer des principes d'exploitation à moins de régler la pêche en fonction des cohortes les moins productives; d'autre part, comme l'espèce *D. gigas* se caractérise par sa croissance rapide et sa mortalité précoce, il est indispensable de mieux connaître son potentiel de reproduction avant de pouvoir donner des avis sur les niveaux d'exploitation conseillés.

RESUMEN

La población de calamar gigante del Golfo de California es evidentemente única con múltiples cohortes. Estas emigran por separado en determinadas ocasiones pero son contemporáneas. Su reclutamiento en los principales caladeros tiene lugar alrededor de mayo cada año. De mayo a septiembre la población presenta las más altas densidades y, en consecuencia, una situación óptima para la pesca.

Las cohortes crecen con distintos índices, según sea la fecha de nacimiento, y probablemente sus tasas naturales de mortalidad son igualmente diversas aun cuando todavía no haya sido posible medir este parámetro por separado para cada cohorte.

Los análisis de evaluación de poblaciones indican que después del desarrollo excesivo de la pesca, la población está llegando al Rendimiento Máximo Sostenido (RMS). Los planes de ordenación son difíciles de definir, a menos que la pesca esté reglamentada en términos de cohortes menos productivas y como el *D. gigas* es una especie de rápido crecimiento y muerte es esencial obtener un mejor conocimiento de su potencial de reproducción antes de dar asesoramiento sobre los niveles de pesca.

1. INTRODUCTION

The Giant or Jumbo squid (*Dosidicus gigas*) is the most abundant of all cephalopod resources within Mexican waters. An extensive fishery based on this species has developed in the last three years mainly in the Gulf of California.

Existing knowledge about the biological characteristics and exploitation of this species is very limited and for this reason, in 1979, the National Fisheries Institute of the Department of Fisheries in Mexico, together with Food and Agriculture Organization of the United Nations (FAO), set up a programme of research into this species in the Mexican Pacific.

The objectives of this programme were:

1. To define the taxonomic position of the species of squid to be found in the Gulf of California and the adjoining Pacific waters.
2. To obtain information about the biological and ecological characteristics of the Giant Squid and in particular about its reproduction; growth, recruitment and mortality patterns.
3. To assess the size of Giant Squid stock in the area.
4. To establish, on the basis of knowledge of its population dynamics, different plans for a rational exploitation of this resource.

Methods:

In order to meet these objectives, a great deal of exploratory work was carried out during 1980 in the area of distribution of this resource in the Gulf of California, using the R/V ANTONIO ALZATE. This multi-purpose vessel, with an overall length of 24 m was equipped with a 12 kW lights system to attract squid, as well as manual and automatic jigging machines. Jiggers of different colors and sizes were used.

The exploratory grid was based on a systematic sampling design. The lights to attract squid were switched on during each station for a period of approximately ten minutes which was then followed by a period of one hour of jigging to catch the squid.

While information on catches and biological features was obtained from the exploratory cruises carried on throughout the year, statistics were also gathered on the composition and characteristics of the commercial fleet, catch and fishing effort, size frequency of the catch and biological information concerning maturity, sex, stomach contents and morphometric details.

2. TAXONOMY

Valid name: *Dosidicus gigas* d'Orbigny, 1835
Objective synonymy: *Ommastrephes gigas*. d'Orbigny, 1935
Ommastrephes giganteus. Gray, 1849
Dosidicus eschrichtii. Steenstrup, 1857
Dosidicus steenstrupii. Pfeffer, 1889
Dosidicus gigas. Hoyle, 1909
Taxonomy: Phylum mollusca; Class Cephalopoda; Sub-class Coleoidea; Order Teuthoidea; Sub-order Oegops ida; Family Ommastrephidae; Subfamily Ommastrephinae; Genus Dosidicus; Species *Dosidicus gigas*.

3. DISTRIBUTION AND MIGRATION

The giant squid, like most ommastrephids, is oceanic, although it also has neritic components. Its general distribution seems to be associated with upwelling zones, being most probably related to small pelagic species that inhabit these areas and which constitute its basic diet.

D. gigas can be found in the eastern Pacific from approximately 36° Lat N to 26° Lat S and westward up to 125° w (Figure 1). The species probably forms different stocks within its general distributional range. Areas with high densities are defined from the Equator to 18° Lat S, in the southern hemisphere, and from 28° Lat N to 16° Lat N including the Gulf of California in the northern hemisphere (Nesis, 1970; Wormuth 1976; Suda, 1973; Sato, 1976) (Figures 2 and 3).

Extensive seasonal migrations have been reported for loliginid and ommastrephid species. Most of these were related to changes in water temperatures. *D. gigas* is not an exception to this rule. It approaches warmer costal areas in summer and autumn and retreats to more oceanic areas in winter (Sato, 1976; Arnold, 1979).

The giant squid population inhabiting the Pacific migrates within Mexican territorial waters and out of the Gulf of California in accordance most probably with feeding and spawning activities. It initiates migration into the Gulf of California in January reaching its northernmost position (29°N) by April. During this time, juveniles and younger adults migrate separately from the adult component. Their migration follows a closer to shore pattern in contrast to the adults which occupy the central and deeper zones of the Gulf. From May to August the stock is mostly found in the upper central section of the Gulf, with a clear stratification by size. At this time adults are located in a strip of about 10 miles wide along the coast while the younger adults are found beyond the 10 mile limit between 26° to 28° Lat N.

Starting in July the stock spreads across towards the eastern side of the Gulf, occupying almost all the central section of it. There is a greater mixing of size components at this time. At the end of August and during the month of September there is a migration in a southern direction towards the entrance to the Gulf.

A small fraction of the stock, formed mainly by older individuals (> 55 cm ML), remains in the upper Gulf during the winter months. Their distribution is confined to the eastern-central portion of the Gulf.

Evidence from exploratory fishing (Sato, 1976) and commercial operations carried out from October to December, show that this squid population, (once outside the Gulf of California) may be divided into two major components. One of them migrates south along the coast and the second to an area in front of the Baja California Peninsula.

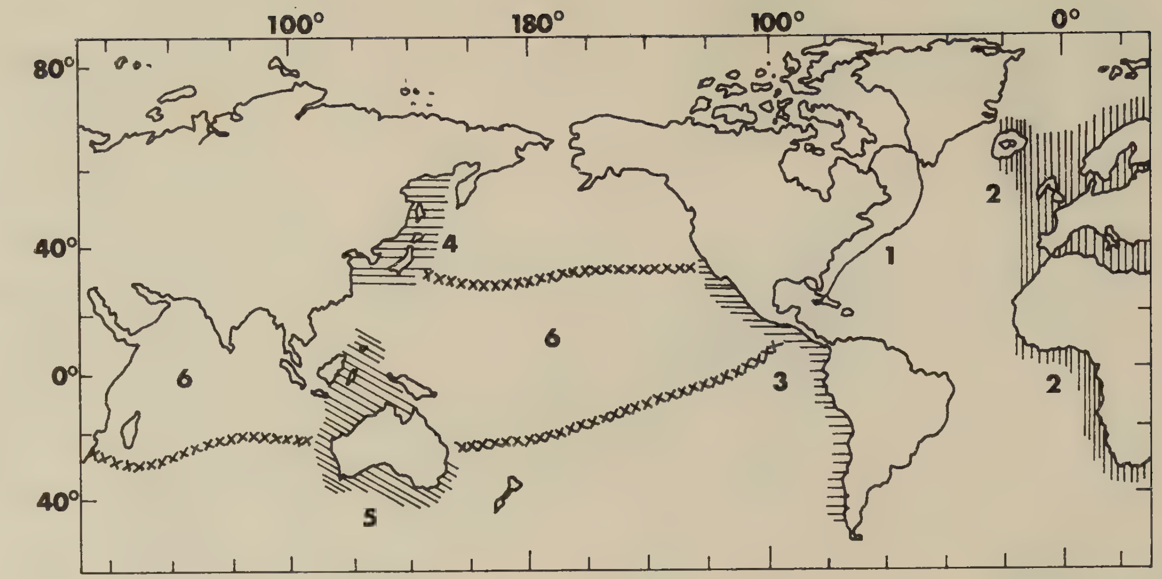
A general migration scheme is given in Figures 4 and 5.

Ommastrephids are commonly found at the surface during the night hours and vertical migrations can extend to several hundred meters (Baker, 1960). *D. gigas* has been observed at the surface at night (Clarke, 1966) and in some occasions even during the day (Roper and Young, 1975). Once in the Gulf of California this species follows a diel migration, coming to the surface at night. During the early migration movement into the Gulf, however, adults have been located hydroacoustically at depths greater than 100 meters. They could be captured with deep lines and jigs at night, but lights did not attract them to the surface.

4. THE FISHERY

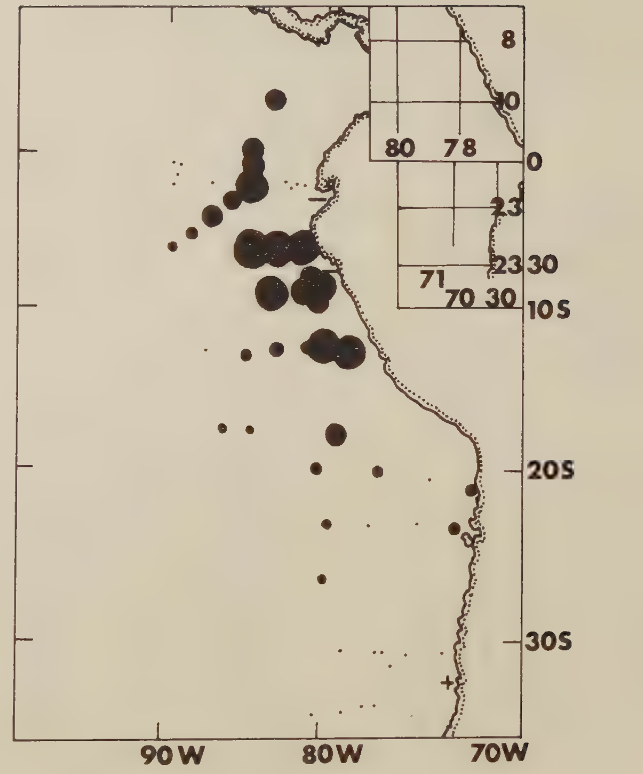
4.1 Historic Production

Fishing for giant squid in the Gulf of California started in 1974 with the operation of a small artisanal fleet, which fished for 2 or 3 months during the summer when stocks wewe closer to shore. Production was very low and the catch was consumed locally.


100°
180°
100°
0°
80°
40°
0°
40°
1
2
2
3
4
5
6
6

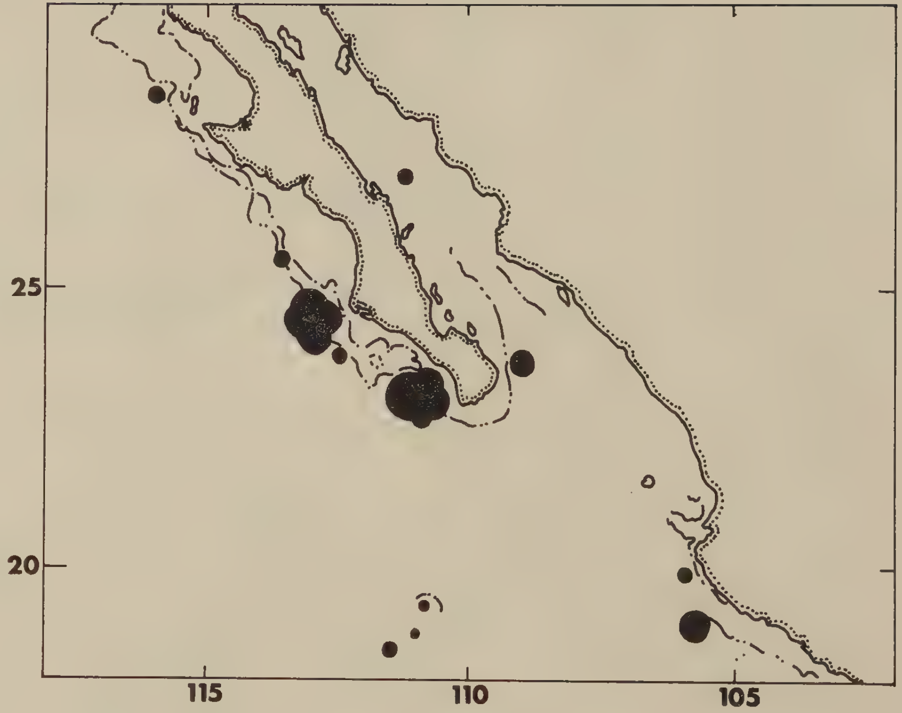
Legend: 1 - *Illex illecebrosus*; 2 - *Todarodes sagittatus*; 3 - *Dosidicus gigas*;
4 - *Todarodes pacificus*; 5 - *Nototodarus sloani gouldi*;
6 - *Symplectoteuthis oualaniensis*

Figure 1 The world distribution of six species of ommastrephid squids (after Suda, 1973)


8
10
80
78
0
23
23 30
71
70 30
10S
20S
30S
90W
80W
70W

Legend:
- • 1 no information
- - 2 none
- + 3 present
- ● 4 single individual
- ● 5 few
- ● 6 moderate numbers
- ● 7 numerous
- ● 8 very numerous

Figure 2 Distribution of *Dosidicus gigas* charted by USRR research vessel, 26 August to 14 September, 1968 (after Nesis, 1970).


25
20
115
110
105

Legend:
- ● 150-300 kg
- ● 300-600 kg
- ● 600-1 200 kg
- ● 1 200-2 400 kg
- ● 2 400-4 800 kg
- ● more than 4 800 kg
- ——— 200 m
- — — — 2 000 m

Figure 3 Relative abundance of catch by area 14 October to 13 December (after Sato, 1976).

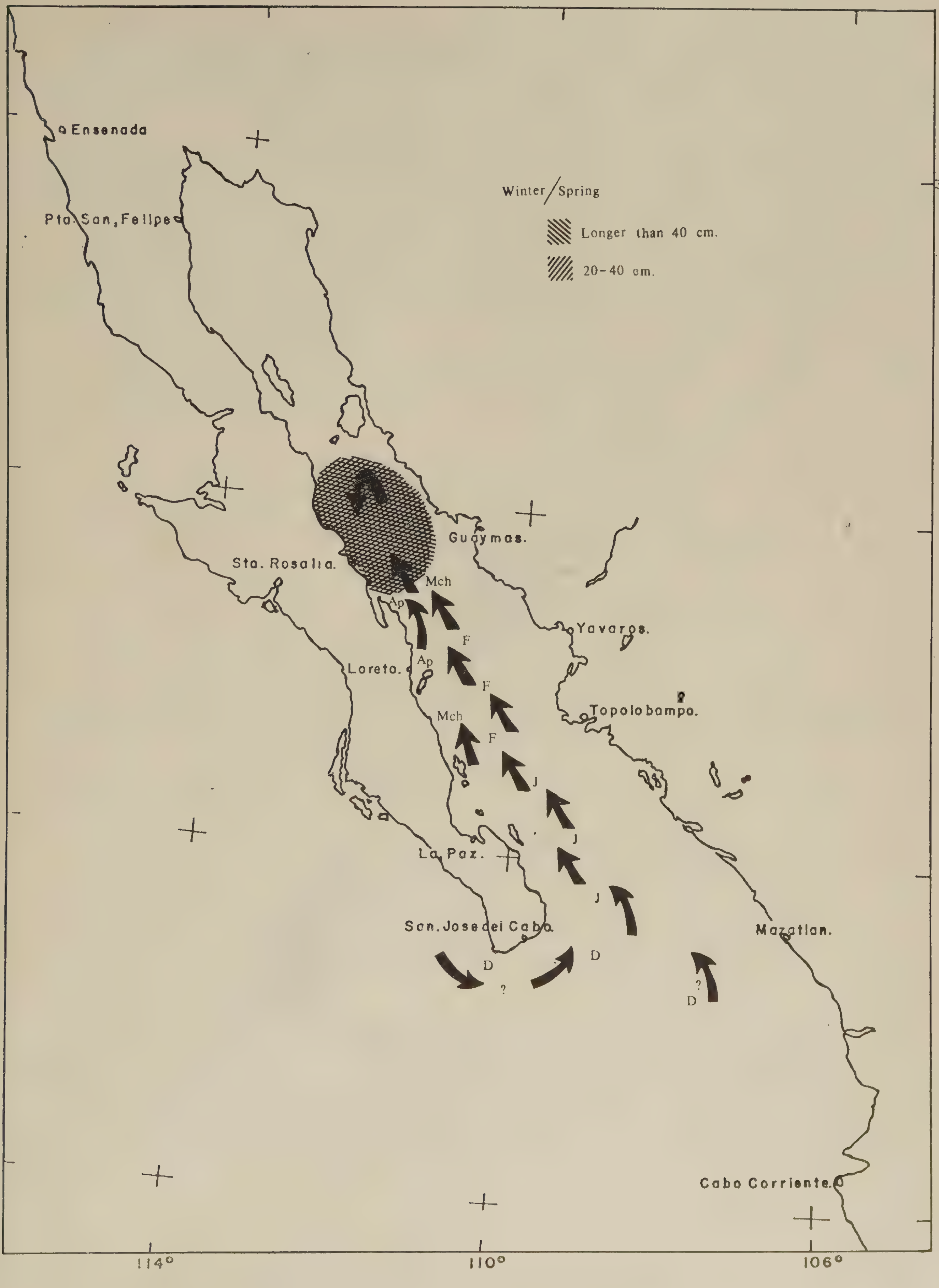

Ensenada
Pta. San, Felipe
Winter/Spring
Longer than 40 cm.
20-40 cm.
Guaymas.
Sta. Rosalia.
Mch
Ap
Yavaros.
F
Loreto.
Ap
F
Topolobampo.
Mch
F
J
J
La Paz.
J
San. Jose del Cabo.
Mazatlan.
D
D
?
?
D
Cabo Corriente.
114°
110°
106°

Figure 4 General migration scheme for *Dosidicus* (winter/spring)

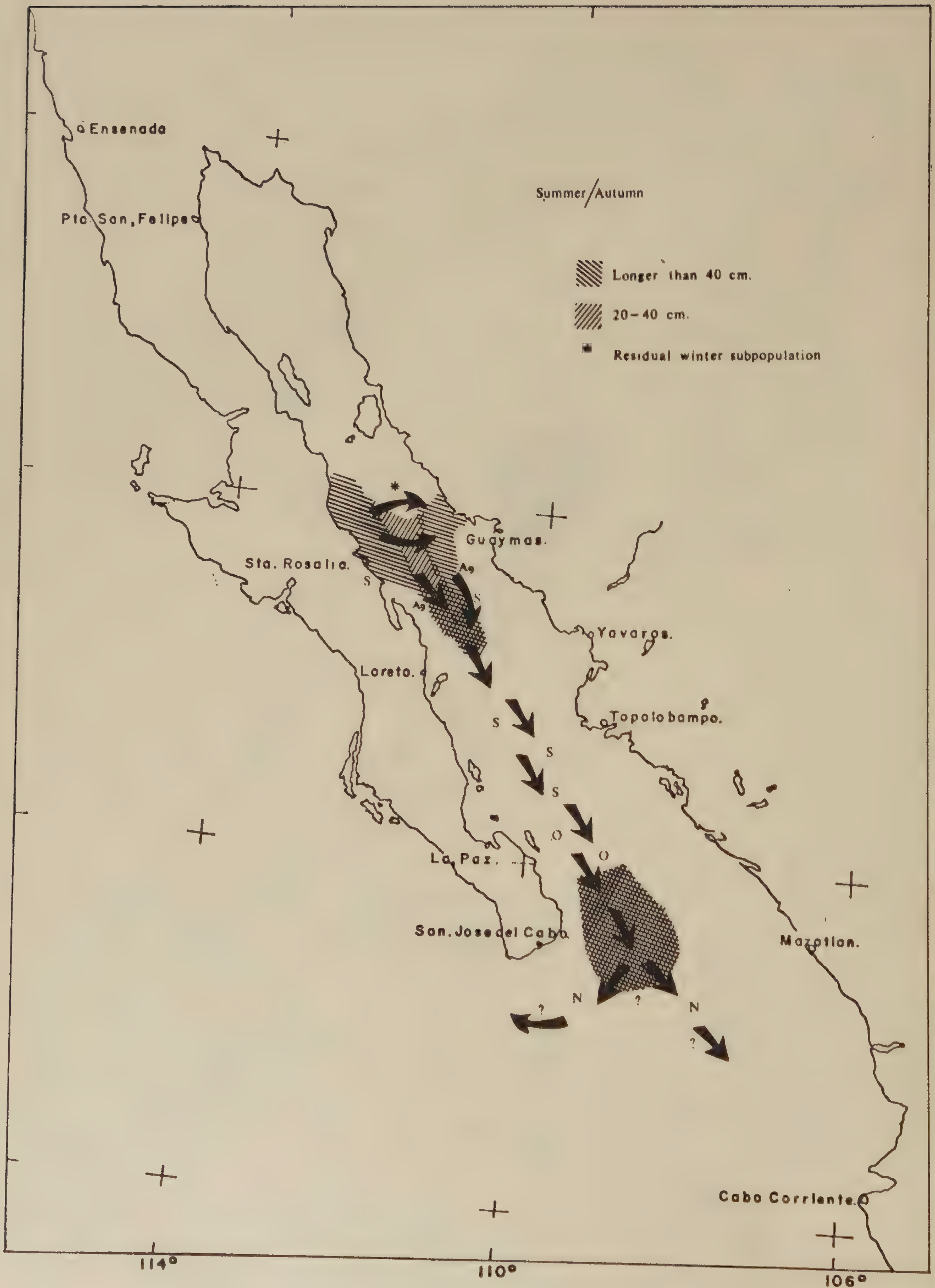

Ensenada
Pto. San, Felipe
Summer/Autumn
Longer than 40 cm.
20–40 cm.
Residual winter subpopulation
Guaymas.
Sta. Rosalia.
S
Ag
Ag
S
Yavaros.
Loreto.
Topolobampo.
S
S
S
O
O
La Paz.
San. Jose del Cabo
Mazatlan.
N
?
N
?
?
Cabo Corriente.
114°
110°
106°

Figure 5 General migration scheme for *Dosidicus* (summer/autumn)

Since 1978 the squid fishery has operated in a complementary fashion to the shrimp fishery which has a closed season during the summer months. Shrimp boats switch to squid fishing during that time.

By 1979 Japanese jigger boats were incorporated into the fishery through joint ventures established with Mexico. These brought new fishing technologies and production was greatly enhanced. Since then several other joint ventures have been formed and consequently the fishery has developed to considerable levels.

During 1980 the state-owned fishery enterprise, Productos Pesqueros Mexicanos, introduced a new policy for the purchase of squid, by which all squid caught by the fleet would be purchased by the enterprise if no other buyers were forthcoming. This purchasing policy attracted greater numbers of shrimpers to the fishery.

During this time, the fishing season has been extended to whole year operations because of the increased operational range of Japanese jigger boats.

Yearly Giant Squid Production is given in the following table. The figures are given in metric tons.

1974	1975	1976	1977	1978	1979	1980 *
14.0	43.4	147.0	300.0	2000.0	5000.0	22000.0

* Figures for the year up until October.

The above table shows that with an annual growth rate averaging 268.2% the fishery has developed very rapidly.

At the international level, the species is not recorded in the annual world statistics of FAO. However, due to the abundance of giant squid along the west coast of South America, it is very likely that production given for unspecified ommastrephids in statistical areas 77 and 78 corresponds to *D. gigas*.

Production in tons for unspecified ommastrephids in the two areas is given in the following table.

	1971	1972	1973	1974	1975	1976	1977	1978
Area 77	----	----	100	73	76	----	40	40
Area 87	500	----	----	----	----	717	1	1

4.2 Fleet and Fishing Gear

The squid fishing fleet is made up of 15 Japanese jigger boats belonging to Mexican-Japanese joint ventures, approximately 200 shrimpers, 10 snapper boats and 20 to 30 small open boats. This fleet can be divided into different categories according to the characteristics of the boats (Table 1). The criteria employed for establishing categories were: vessel size, which determines the power of the light attraction system used, crew size and the modus operandi which is in direct relation to the length of fishing trips and the type of product unloaded.

Table 1. Vessel categories

	Category 1 Open boats	Category 2 Snapper boats	Category 3 Shrimp boats type I	Category 4 Shrimp boat type II	Category 5 Small Japanese jigger boats	Category 6 Large Japanes jigger boats
length overall (m)	6 - 8	16	23 - 25	same characteristics as in previous category. Difference lies in the number of crew members being 10 to 12 and the length fishing trips which are one day operations in which whole squid is unloaded fresh.	35 - 40	48 - 52
hull	fiber glass	fiber glass	steel or wood		steel	steel
fish hold capacity	2 - 3 tons	30 m^3	50 m^3		300 m^3	500 m^3
engine (hp)	outboard, 40 - 50	inboard, 230	350 - 480		up to 1,000	up to 1000
crew size	2 - 3	6	7 - 9		15 - 20	15 - 20
length of fishing trips	1 night	12 - 20 days	20 - 25 days		15 - 40 days	15 - 40 days
light attraction system	1 - 2 gasoline lamps	5 - 8 100 watt lamps	lamps, variable up to 1 kW total one line-one jig per fisherman, Japanese and locally built jigs		up to 150 kW	up to 250 kW
fishing gear	one line-one jig per fisherman	one line-one jig per fisherman, Japanese and locally built jigs			24 x 2 drum automatic jigging machines 8 - 25 Japanese jigs per line	24 x 2 drum automatic jigging machines 8 - 25 jigs per line
product conservation	none	ice	refrigerated ice		frozen	frozen
product type	eviscerated, fresh	eviscerated, fresh	eviscerated, fresh		frozen mantles in 15 kg boxes	frozen mantles in 15 kg boxes

Jigs used by the fleet are of two types: Japanese jigs with two steel hook crowns, 12 cm body size, 12 and 18 mm hook size, and locally built jigs made out of aluminium tube which have a body length of 30 cm and with nail crowns as hooks.

The lines in the automatic jigging machines are made of 0.8 - 1.2 mm diameter nylon, with Japanese jigs are spaced 0.80 to 1.2 metres apart. The number of jigs used per line depends on squid size and density.

4.3 Fishing Power, Jig Efficiency and Selectivity

Squid catch per unit of effort is affected by the catching efficiency of the fishing gear used and population density in the fishing area. In this way the fishing power of a vessel, relative to squid catchability, will depend on several factors. Among these are size and color of the jigs, length of the hooks, number of hook crowns per jig, number jig per line, number of lines per vessel and characteristics of the light system used to attract and concentrate the resources.

In general the method used to determine fishing power, or to assess any fishing efficiency factor, is that based on an analysis of a variance model as described by Robson (1966) and derived from the catch equation:

$$C_{ij} = q_i \, f_{ij} \, \bar{N}_j \, \varepsilon_{ij}$$

where C_{ij} = catch realized by one element of class i, operating in an area-date combination j. Elements in class i could be boat categories, jig types. etcetera

q_i = catchability coefficient of an element of class i and defined as the fraction of the stock captured per unit of effort of the element of class i

f_{ij} = fishing effort of element of class i in the area-date strata j

$\bar{N}_j$ = average population abundance in area-date strata j

εij = random error.

Catch per unit of effort for one element of class i (vessel, jig, etcetera) in area-date j is defined from the catch equation above as:

$$C_{ij} / f_{ij} = q_i \, \bar{N}_j \, \varepsilon_{ij}$$

Since the absolute values for $\bar{N}_j$ and q_i are not usually known, in order to solve the above equation it is necessary to define relative values in terms of some class i in an area-date j chosen as standard (s). For this purpose, if we define $P_i = q_i / q_s$ and $D_j = \bar{N}_j / \bar{N}_s$ where s refers to a standard class-area-date, then the previous equation will be

$$C_{ij} / f_{ij} = q_s \, (q_i / q_s) \, \bar{N}_s \, (\bar{N}_j / \bar{N}_s) \, \varepsilon_{ij}$$

transforming logarithmically

$$\log (C_{ij} / f_{ij}) = \log q_s + \log \bar{N}_s + (\log q_i - \log q_s) + (\log \bar{N}_j - \log \bar{N}_s) + \log \varepsilon_{ij}$$

this last equation in terms of analysis of variance (ANOVA) is equivalent to

$$Y_{ij} = \alpha_s + \beta_s + (\alpha_i - \alpha_s) + (\beta_j - \beta_s) + n_{ij}$$

or

$$Y_{ij} = \mu + \alpha'_i + \beta'_j + n_{ij}$$

where $\mu = \alpha_s + \beta_s = \log q_s + \log \bar{N}_s$

$\beta'_j = (\beta_i - \beta_s) = \log \bar{N}_j - \log \bar{N}_s$

$\alpha'_i = (\alpha_i - \alpha_s) = \log q_i - \log q_s$

$n_{ij} = \log \varepsilon_{ij}$

In this way the ANOVA model is used to estimate the α'_i effects as efficiencies of elements in class i with respect to a standard element of class s, and the β'_j effects as relative population densities in a standard area-date j referred to a standard s.

The treatment effects (α'_i and β'_j) in the above ANOVA model were estimated by the use of a computer routine given by Abramson (1971).

4.3.1 Fishing power estimates

Fishing power estimates for different vessel categories were obtained from a representative sample of the squid fishing fleet. The categories are defined and described in section 4.2.

This analysis used information on catch in kilograms per night of operation, realized for each vessel category in the main squid fishing grounds in the west central part of the Gulf of California and for the months of March to August 1980.

Results are shown in the table below and in figure 6 where category 1 was arbitrarily chosen as standard.

CATEGORIES	1	2	3	4	5	6
FISHING POWER	1.000	1.501	1.496	6.524	11.144	28.015

Differences in relative fishing power estimates are not only related to boat size, but also to mode of operation.

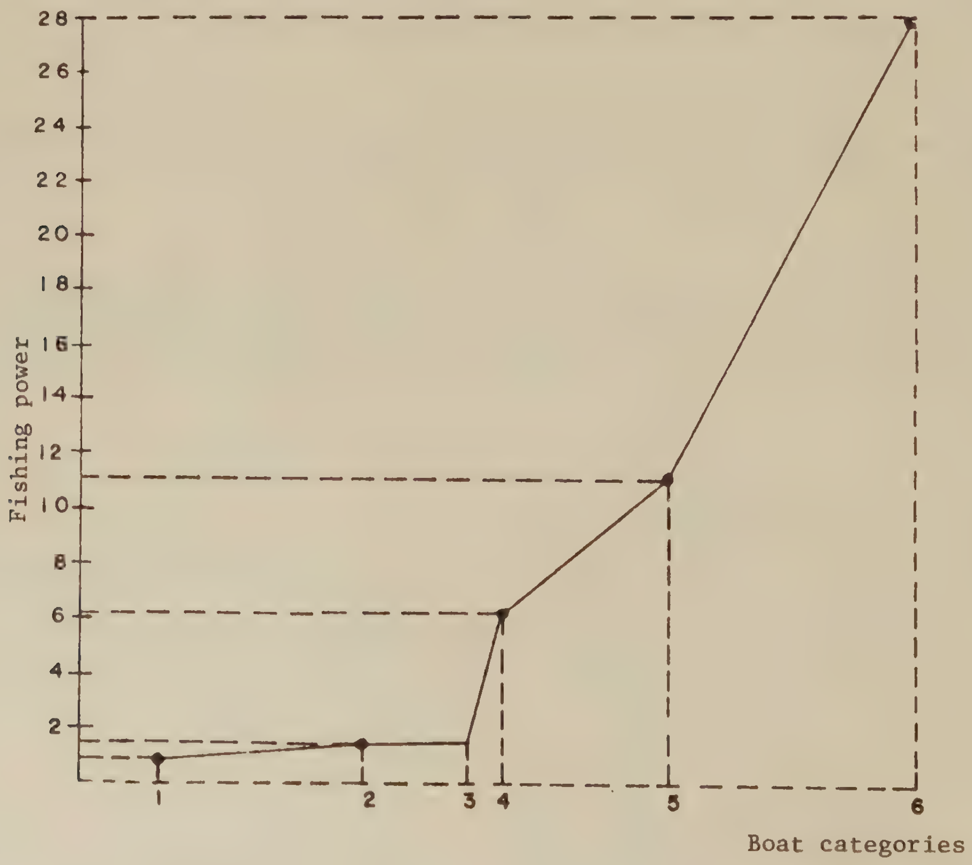


Figure 6 Distribution of fishing power estimates by boat category

Categories 1, 2, 3 and 4 catch squid with hand lines so that similarities in categories 2 and 3 are related approximately to the number of fishermen participating in the catching process. Differences between categories 3 and 4, even when they are boats of the same size, are due to the catching time lost in category 3 where the catch is cleaned and stored in ice, while in the other category whole squid is packed in ice and transported like that on one-day trips.

4.3.2 Jig efficiency

Jigs of different colors have different catchability effects depending on the squid color preference, thus creating differences in the catching efficiency.

To estimate the relative jig efficiencies due to colors, an experiment was conducted during the month of January 1980. During this experiment jigs of five different colors of equal size and number were used. Catches by each of the colours were recorded separately. The standarized information was number of squids caught by different jig type per minute.

Relative efficiencies are given in the following table:

	TRANSPARENT	GREEN	RED	PINK	SILVER
RELATIVE EFFICIENCY	1.000	0.536	0.938	0.792	0.472

From the estimated values given in the above table it can be seen that transparent jigs are the most efficient followed by red and pink. Green and silver jigs are at about 50% efficiency with respect to the standard.

4.3.3 Selectivity

The probability that a squid of a given size is caught upon encountering a jig of specified construction determines that jig's selectivity. In Figure 7 size frequency distributions are shown for squids caught with japanese-type jigs and large locally made jigs. From the figure it can be drawn that both types of jigs are catching about the same range of sizes, thus not allowing for estimating selectivity by indirect methods. This is due to the fact that small individuals are equally caught with small as with large jigs, and at the same time larger individuals are still caught with small jigs.

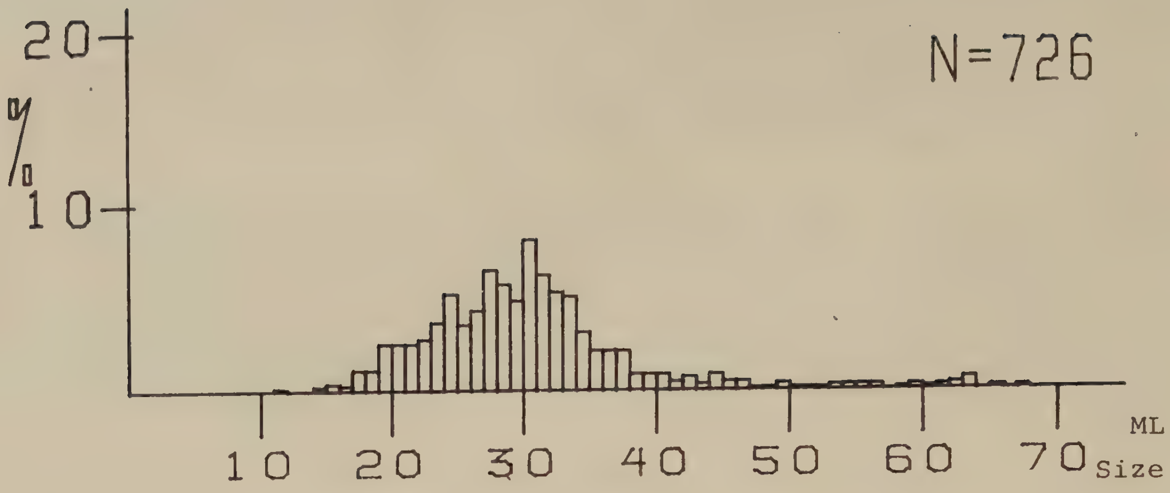
The difference in numbers of larger individuals caught with small jigs is due to losses experienced with this type of jigs and attributed to an excess weight of larger individuals for smaller hooks.

It can be concluded that selectivity of the two types of jigs used in the fishery is similar for a size range of 12 to 47 cm ML, and if larger hooks were introduced with Japanese type jigs probably the number of larger individuals retained will equal those captured with locally built jigs. Jig selectivity for giant squid is then a function of hook size as a capacity to retain weight rather than factors associated with jig body size.

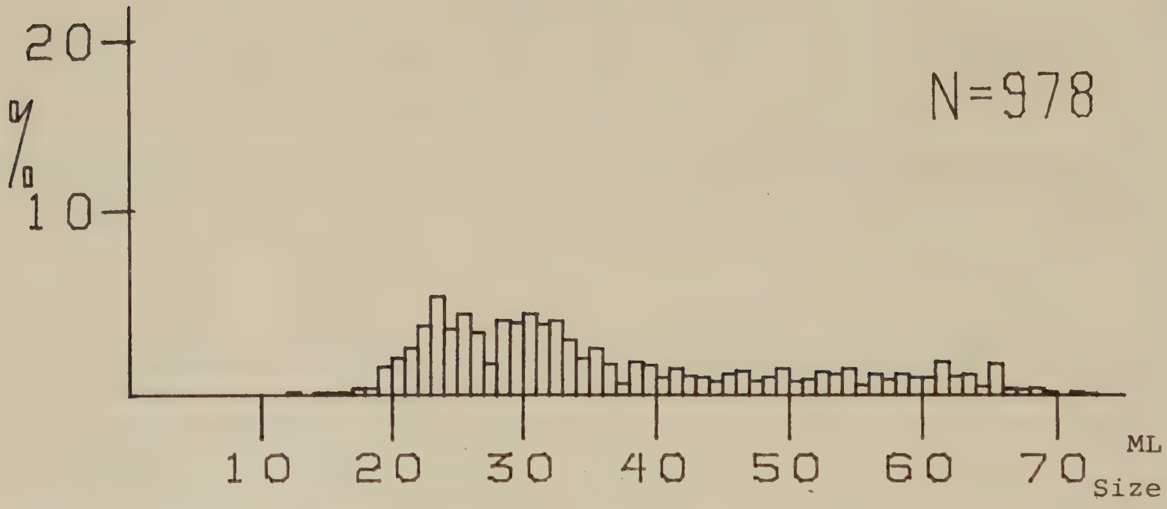
5. BIOLOGY

5.1 Feeding

Most authors have agreed that *D. gigas* is an active predator at all stages of its life. Fitch (1968), reports that stomach samples from individuals of 9 to 50 cm ML taken in Mexican and Costa Rican waters as well as samples of squid found on the beaches of California, showed that giant squid attack almost any prey available. The composition of the diet is size dependent according to the following results:



Japanese-type jigs.



Large locally made jigs.

Figure 7 Size frequency distributions for squids caught with Japanese type jigs and large locally made jigs.

small individuals	mostly crustacean
medium size	fish (mainly pelagic)
large individuals	squid (same species included)

In southern California giant squid feeds mainly on Engraulidae, Myctophidae, Scorpaenidae and Embiotocidae. Nesis (op. cit.) reports that the diet of the giant squid living off the coast of Peru and Chile consists of:

Myctophides	70.2%
Squid	13,3%
Plankton	7.9%
Saury	1,2%
Others	1,6%
Digested unidentified food items	5,8%

Sato (1976) reports pelagic red crab (*Pleuroncodes planipes*) to be the main component of the diet of *D. gigas* in the Pacific off the Baja California Peninsula. Other food items found in smaller amounts were: Nyctophids, Engraulids, Carangids and large quantities of unidentified larvae.

Qualitative examinations of the stomach contents of squid found in the Gulf of California area have shown that their diet is made up mainly of sardines (*S. sagax caeruleus*) mackerel (*Scomber japonicus*) and red crab (*P. planipes*).

During May and July the favourite diet of giant squid seems to be penaeid post-larvae which are attracted by light during the fishing process. Organisms longer than 65 cm ML with more than 500 g of shrimp larvae in their stomach have been captured.

Their predilection for these larvae makes squid ignore jigs used at the surface but not those used between 5 and 6 metres below the surface.

In areas of intensive fishing it has been shown conclusively that the squid feeds mainly on its own species. What occurs perhaps is that squid which have been badly wounded by the jigs escape and, weakened, are then attacked by their own kind.

As far as the quantity of food-matter found in the stomachs, most of the specimens caught were found to have empty stomachs or to contain already digested material. Specimens found to have full or partly full stomachs (mostly with the same species) all measured more than 60 cm ML. It can be concluded from the preceding information that this species is a very voracious predator in which high levels of cannibalism are observed when intensive fishing is performed or when no other food but squid is available.

The large percentage of empty stomachs observed could possible indicate very high digestion rate, or a low abundance of available food, but this seems quite unlikely because of the great stocks of pelagic fishes of the Gulf of California.

D. gigas distribution is generally associated with pelagic resources of the west coast of America, the Peruvian anchovy in Chile and Peru, the Californian anchovy in the west coast of Baja California and sardines and mackerel in the Gulf of California.

In the areas where upwellings are not strong enough to support large populations of pelagic fishes the principal diet consist of bathypelagic fishes, particularly Myctophids. Due to their small size-20 to 30 mm- they represent an easy prey for squid.

5.2 Sexual Maturity

Very little is known about the reproductive cycle of *D. gigas*. Nesis (op. cit.) reports that off the coast of Peru and Chile, males of the species begin the process of maturation when they have reached 20 to 25 cm ML. At a length of more than 29-30 cm ML all specimens have reached maturity. Females do not begin this cycle until a larger size of 36-37 cm ML has been reached, full maturity being seen in those which measure more than 40 cm ML.

Mating in *D. gigas* as in most Ommastrephids, occurs in a head-to-head position. Male spernatophores are transferred to the female buccal membrane where seminal receptacles are arranged forming a ring around the mouth. Number and size of spermatophores increase as males grow in size. Individuals measuring 24 cm ML have 300 spermatophores with an average length of 27.5 mm, while males measuring 40 cm Ml were found to have 1,200 spermatophores with an average length of 35 mm. The fecundity of females ranges from 1,000,000 to more than 6,000,000 eggs.

For this sexual maturity study 1,631 females were sampled with the purpose of defining spawning time, spawning areas and size at first maturity.

Monthly percentages of mature individuals are shown in Figure 8. From this figure, it can be seen that for the months of December and January the highest percentages correspond to mature individuals (Phase III, being 70.8% and 31.1% respectively, indicating that a spawning period occurs during early winter. This spawning has a great importance because it will generate the individuals heavily fished from May through September that recruit to the fishery in March and April.

During most of the year mature females can be found in some abundance, as well as juveniles (5-15 cm ML). The high percentage of spent females observed in May and June suggests a spawning activity during those months generating the individuals that will recruit in September. There is also a peak of mature females in September, whose progeny will enter the fishery in January and February.

In relation to spawning areas, mature squids could be observed in winter in the northeast Gulf of California near Guaymas, but most of the population would spawn in the Pacific waters off the Baja California Peninsula at the edge of the continental shelf. In summer the spawning area is located in the Gulf of California near Santa Rosalia where most of the stock is concentrated.

Size at first maturity is dependent on food availability and temperature but it ranges from 35 to 40 cm ML in females (4-6 months old) and from 18 to 25 cm ML in males (2-3 months old).

It appears that the reproductive cycle is not seasonally fixed and that changes in oceanographic conditions in the Gulf of California and adjacent waters have a great influence in determining the reproductive peaks of *D. gigas*.

5.3 Age and Growth

5.3.1. Antecedents

Research into the age and growth in cephalopods is scarce and limited to very few species. This is due to extreme difficulties of ageing cephalopods since they are lacking suitable hard bony parts where annual or other time related checks can be registered as changes in their metabolism. It is generally accepted that squids grow extremely fast and that most species very seldom live more than 2 years.

Age and growth estimates for *D. gigas* are given by Nesis (op.cit.). He defined three mantle length (ML) ranges corresponding to small (20-33 cm), medium (34-45 cm) and large (> 46 cm) individuals and correspondingly assigned ages 1, 2 and 3-4 years to each of the size ranges. Monthly growth rates were given from the above relationship as 2-2.5 cm during the first year of age and 1-1.2 cm for the second year.

The same author mentions ML's for larvae ranging between 1.9 and 9.5 mm. One identified post larvae measured 14 mm.

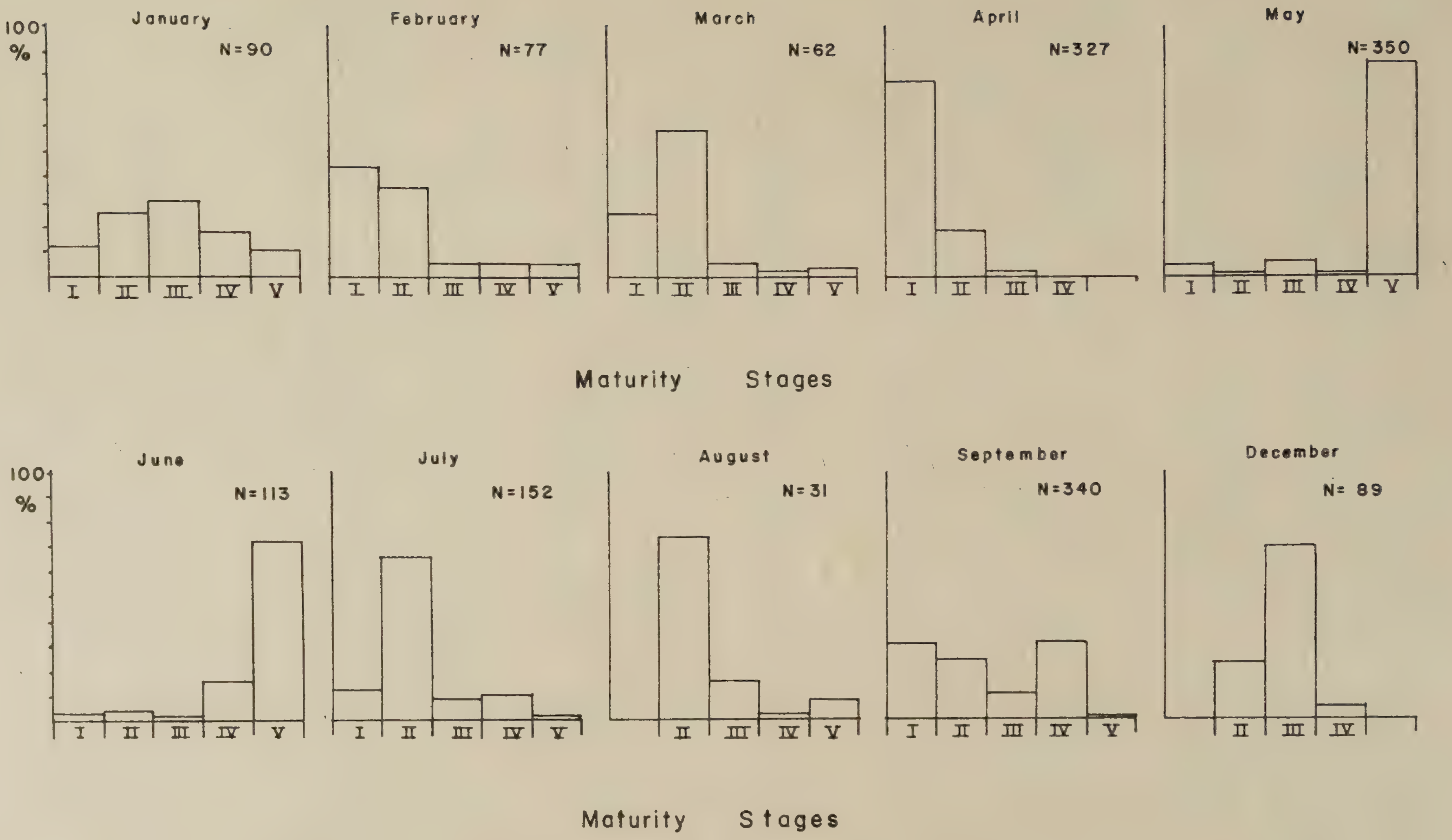


Figure 8 Relative importance of the Females Maturity Stages by sampling month 1980.

Larvae growth for loliginids and similarly for ommastrephids probably does not exceed 4 to 5 mm ML per month (Arnold, 1979; Fields, 1965; Hurley, 1976), increasing later to 10-20 mm/month. Some species may reach a growth rate of up to 30-40 mm/month (Araya and Ishii, 1974; Holme, 1974). These growth rates may change in accordance with different seasons of the year. Murata and Ishii (1977) give growth rates for *Ommastrephes bartrami* as 30-40 mm/month during summer, 10-20 mm/month in fall and decreasing to 5-10 mm/month in winter.

Fridriksson (1943) gives growth rates for *Todarodes sagittatus* as 76 mm/month in July, 52 mm/month in August, 28 mm/month in October and 22 mm/month in winter. Arnold (op. cit.) gives information for *Loligo forbesi* as 37 mm/month for males and 27 mm/month for females during summer and autumn months.

Maximum size reported for *D. gigas* varies in accordance with latitude and hemisphere. Nesis (op. cit.) gives 65 cm ML as maximum for the equatorial Pacific, while, from a morphometric relationship between rostral beak length and mantle length and information on beak size the same author mentions that is possible to find a maximum ML of over one metre. García-tello (1965) reports 93 cm and 33-35 kg as maximum ML and total weight for *D. gigas* in Chile. Clarke (1966) reports 365 cm maximum total mantle length for the same species and country. Berry (1962 b.) and Phillips (1961) give 152 cm as maximum observed total length and 13.6 kg total weight for *D. gigas* in California. Wormuth (1970) reports about geographical size variability in *D. gigas*, being very seldom greater than 40 cm ML in collections from the northern hemisphere while they can reach up to 150 cm in Peru.

5.3.2 Age and growth of *D. gigas* in the Gulf of California

Age and growth studies for *D. gigas* from the Gulf of California were conducted with information on mantle length frequency distributions obtained monthly in exploratory cruises.

A method for analysis of polymodal frequency distributions proposed by Yong and Skillman (1975) was used to separate growth components. With this purpose observed data on length frequencies are transformed into probits similar to techniques given by Harding (1949) and Cassie (1954). A polynomial regression of degree n is then performed on the probits to obtain a mathematical equation that describes the probit curve. The inflection points which are estimates of the points of overlap of the distributions, are found by taking the second derivative of the descriptive equation and obtaining the real roots.

These cut-off points are then used to separate the different components by the method of steepest descent given by Hasselblad (1966). In this way each of the size component distributions identified are represented by a normal curve.

Average size for each of the identified normal components are shown with an arrow in Figure 9. Following these average values through time it was possible to identify different cohorts and their growth by month. Age was assigned to length by fitting a von Bertalanffy (1938) growth function to the observed data and adjusting the function as close to zero as possible.

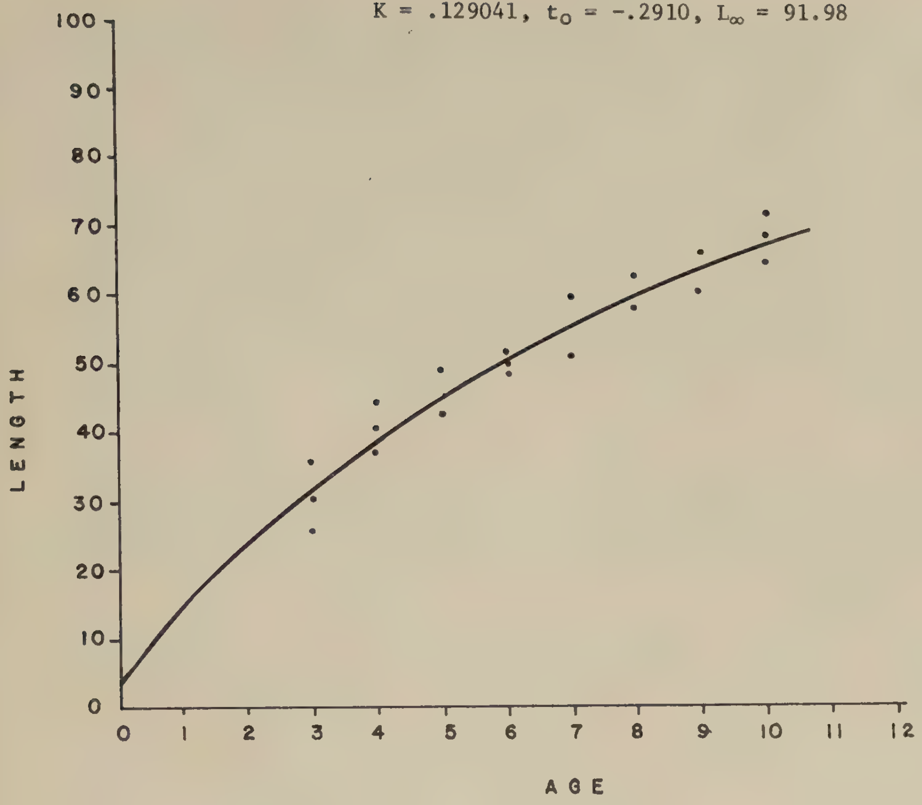
The equation is as usual

$$L_t = L_\infty \left(1 - e^{-K(t - t_o)} \right)$$

where L_∞, K and t_o, parameters of the above equation, were estimated through a least square procedure (Tomlinson and Abramson, 1961).

Five cohorts were identified through the above procedure. Results for the cohorts 1, 3 and 5 are given in the Figures 9, 10 and 11 respectively.

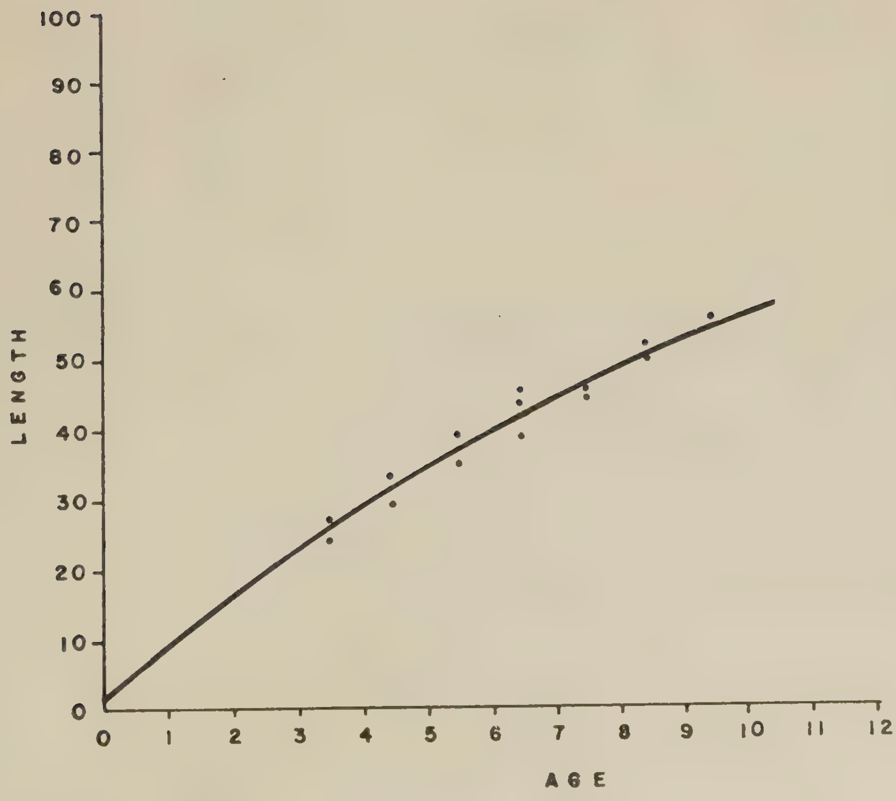
For cohorts 2 and 4 a linear relationship between age and size was found (see e.g. Figure 12).



Cohort 1

K = .129041, t_o = -.2910, L_∞ = 91.98

Figure 9 Growth curve for Cohort 1
Age given in months and mantle length given in cm



Cohort 3

K = .081336, t_o = -.2296, L_∞ = 99.91

Figure 10 Growth curve for Cohort 3
Age given in months and mantle length given in cm

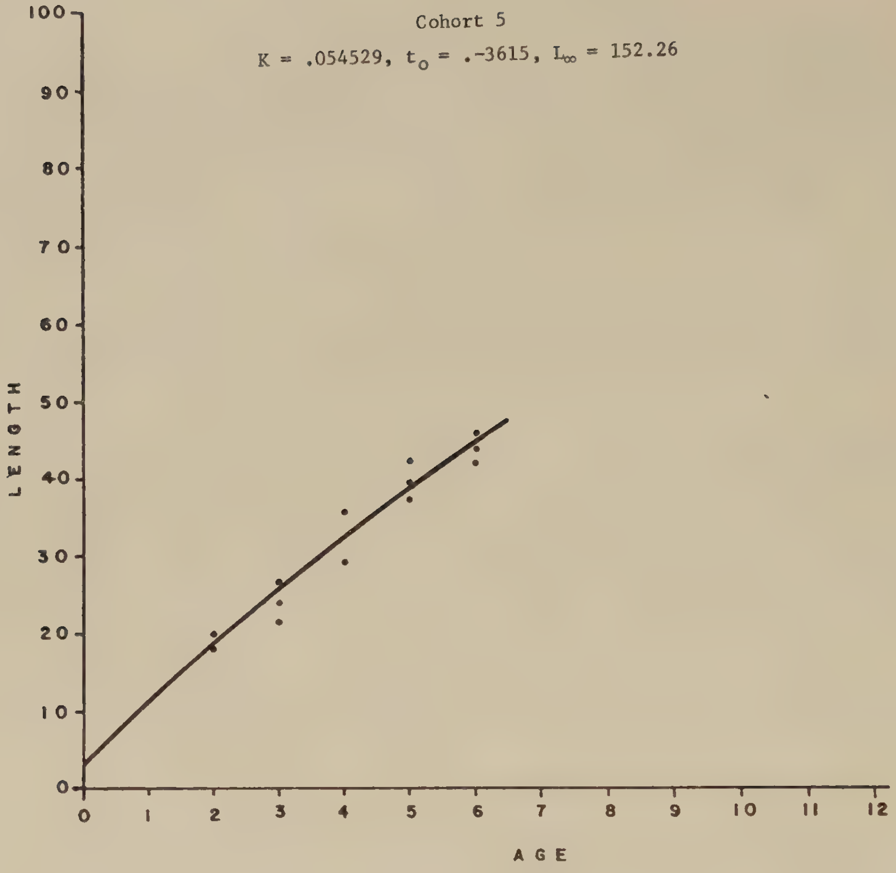


Figure 11 Growth curve for Cohort 5
Age given in months and mantle length given in cm

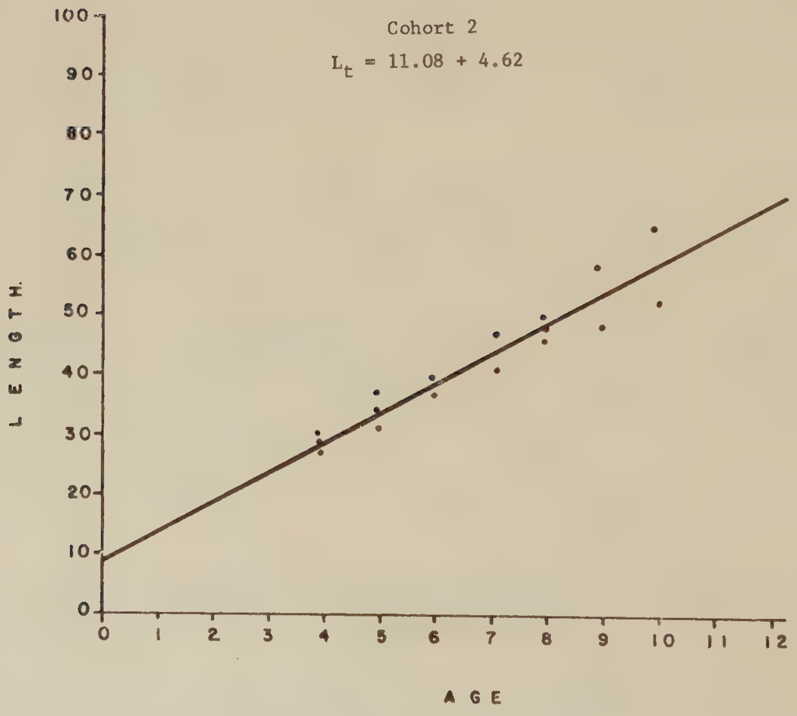


Figure 12 Growth curve for Cohort 2
Age given in months and mantle length given in cm

From the figures and growth equation parameters it is possible to define different growth patterns for each of the cohorts. Thus cohort 1 has a birth date in September and undergoes fast growing during the first four months of life. As such it has a high growth rate ($K = 0.129$). Cohort 2 is born in October and recruited in February. It was not possible to fit the von Bertalanffy growth model to the data because of the erratic monthly growth rates, but a linear regression gave a good fit for the size range observed. Cohort 3 is born during winter and juveniles having a faster growth starting in spring thus having a lower growth rate ($K = 0.081$). Cohort 4 has a birth date in December and appears in the fishery in March and April presenting a very fast growth rate which could not be adjusted to a von Bertalanffy model. As in cohort 2 a linear regression model was applied with good results. Cohort 5 is born in March and thus has an optimum condition for growing. In effect this cohort grows almost linearly. Growth rate is lower than in the previous cohorts ($K = 0.054$). This situation is due to the flattened shape of the curve, lower t_0 value and lack of model fit.

Asymptotic lengths (L_∞) for cohorts 1 and 3 are reasonable, considering that the maximum observed length during fishing explorations has been 75 cm ML. The value of $L_\infty = 152.26$ for cohort 5 is not realistic, and is due to the linear growth already mentioned and a lack of fit of the growth to an asymptotic growth pattern. As such, the growth equation expressed by the estimated parameters for cohort 5 is valid only for the range of observed lengths.

The same effect of linear growth is observed in cohorts 2 and 4 and the results are valid for lengths observed during the period of this study.

Observed growth rates by age have been estimated for each cohort as:

Cohort 1:	1-4 months	9 cm/month
	5-7 months	5 cm/month
	8-9 months	4 cm/month
	7-10 months	1-2 cm/month
Cohort 2:	1-5 months	5 cm/month
	6 months	6 cm/month
	7-8 months	5 cm/month
Cohort 3:	1-4 months	7 cm/month
	5-6 months	5 cm/month
Cohort 4:	1-2 months	6 cm/month
	3 months	2 cm/month
	4-5 months	7 cm/month
	6-8 months	4 cm/month
Cohort 5:	3-5 months	8 cm/month

From these observed growth rates it is easy to conclude that *D. gigas* is a very fast-growing animal, comparable with other oceanic ommastrephids. The higher rates obtained for this species are reasonable given the fact that the waters of the Gulf of California present high temperatures and high food availability almost all year round.

At the same time, from the growth patterns it is evident that *D. gigas* probably does not live more than 18-20 months when growth is becoming asymptotic.

Length-weight relationships valid for a range of 18-72 cm ML are given below for total weight (W_T), mantle weight (W_M) and mantle and head weight (W_{M+H}).

$$W_T = 0.02646165\ \mathrm{ML}^{2.989379}$$

$$W_M = 0.01775312\ \mathrm{ML}^{2.940475}$$

$$W_{M+H} = 0.02503828\ \mathrm{ML}^{2.937908}$$

The exponents in the above relationships suggest isometric growth.

5.4 Natural Mortality Rates

Natural mortality rate estimates for *D. gigas* have not been published. These rates, however, must be quite high because of such factors as:

- the longevity of the species, which in most cases could not exceed two years;
- the fact that, like most cephalopods, it is a species found at intermediary trophic levels, and is thus particularly prone to predation, especially during its juvenile life, and
- the marked frequency of cannibalism which has been observed in the species and which is also commonly seen in various other species of cephalopods.

In general, estimates for the natural mortality rates of cephalopods have been made on the basis of the longevity of the species. The problems presented by the difficulty in determining age with sufficient accuracy have made it impossible to use other methods to estimate mortality, especially those which use population structures.

Thus the best way to estimate natural mortality is by "indirect" methods which use physiological information rather than population sizes.

There are necessarily minimal and maximal natural mortality rates which vary according to the stage of life of the individual specimen. Maximum rates occur at the larval and juvenile stages and in later life, particularly after spawning. However, if the longevity of the species in natural conditions remains relatively constant, then it can be supposed that the squid population has a constant natural mortality rate which gives the longevity which has been observed, and therefore causes a distribution in time of natural mortality rates which is similar to that of the real, but unknown rates.

Taylor (1958) suggested that the maximum age attainable by individual specimens in a population occurs when they have reached 95 percent of their asymptotic length (L_∞) using von Bertalanffy's growth equation, that is:

$$\frac{L_t}{L_\infty} = 0.95 = 1 - e^{-K(t - t_0)}$$

which gives t_M; the maximum age is thus equal to:

$$t_M = t_0 + \frac{2.9957}{K}$$

He estimates the natural rate of mortality as follows:

$$M = \frac{2.9957}{t_M}$$

Furthermore, Allen (1971), postulated that if survival is exponential, generating over time the same longevity:

$$Z = M = \frac{1}{t}$$

in which t is the maximum age attainable by a species.

From information on growth of the giant squid, we see that *D. gigas* may live for a maximum of 16-20 months. According to Taylor's method and the parameters for K and t_0 determined for two cohorts, when $K = 0.129641$ and $t_0 = -0.291$, the squid would live for 22 months minimum and when $K = 0.81336$ and $t_0 = -0.2296$ a maximum of 37 months.

Accordingly, if the above-mentioned values for t, as calculated, are used, the two previously mentioned methods would give the following natural mortality rates (M):

Author	(t)	M (monthly)
Allen	16-20 months	0.0500-0.0625
Taylor	23-37 months	0.0810-0.1302

If one considers that growth studies would suggest that a maximum age of 37 months for the species is an overestimate, then one may suppose that the average monthly natural mortality rate (M) lies between the values 0.05 and 0.08 (0.6-0.96 a year).

6. STOCK ANALYSIS

6.1 DeLury Estimates

Delury (1947) developed a method based on the concept of employing the decrease in catch per unit of effort and accumulative effort for estimating initial population size (N_0) and catchability coefficient (q).

The model assumes a closed population, that catchability is constant for the population from individual to individual, and also constant over time, that time periods are small and natural mortality is zero during the periods.

Braaten (1968) further developed the method to allow adjustment for effort when catch is removed in the time interval.

The adjusted DeLury equation is:

$$\ln (C/f)_i = \ln q N_0 - q \left(\sum_{j=1}^{i-1} f_j + \frac{f_i}{2} \right)$$

where: C = catch in numbers
f = fishing effort
q = catchability coefficient
N_0 = initial population size

This equation is used as a linear regression model

where $Y_i = \ln (C/f)_i$

and $X_i = \left(\sum_{j=1}^{i-1} f_j + \frac{f_i}{2} \right)$: giving estimates of intercept $a = \ln q N_0$ and slope $b = q$ through usual least-square procedures.

Initial population size is estimated as:

$$N_0 = \frac{e^a}{-b}$$

Data used for the analysis consisted of total standardized monthly fishing effort and total monthly catch in numbers estimated from landings in weight and monthly weight frequency distributions. These latter distributions were obtained from the length relationship as expressed in section 5.3.2; this same relationship was used to assign number of individuals caught to length classes. Number of individuals caught from different cohorts were obtained from number of individuals by length class and age-length relationships of the different cohorts as expressed in section 5.3.2. Table 2 shows the data arranged by cohorts and months.

Table 2

Data for DeLury analyses

Month	Age	Catch in numbers	cpue	ln cpue	$\sum_{j=1}^{i-1} f_j + \frac{f_i}{2}$
COHORT 1					
Jan.[a]	3	12 226	23.20	3.14	263.5
Feb.	4	28 708	112.14	4.72	655.0
Mar.	5	47 822	55.41	4.01	1 214.5
Apr.	6	67 097	49.26	3.90	2 327.0
May[a]	7	3 025	1.49	0.40	4 020.0
June[a]	8	29 760	3.76	1.32	8 992.0
July	9	157 368	18.70	2.93	17 159.5
Aug.	10	62 198	12.55	2.53	23 845.5
Sep.	11	30 319	7.66	2.04	28 304.0
COHORT 2					
Feb.	3	5 901	23.05	3.14	128.0
Mar.	4	44 886	52.01	3.95	687.5
Apr.	5	14 833	10.89	2.39	1 800.0
May	6	51 024	25.13	3.22	3 493.0
June	7	31 186	3.94	1.37	8 465.0
July	8	201 040	23.89	3.17	16 632.5
Aug.	9	102 494	20.68	3.03	23 118.5
COHORT 3					
Mar.[a]	3	84 032	97.37	4.58	431.5
Apr.	4	418 819	307.50	5.73	1 544.0
May	5	482 315	238.30	5.47	3 237.0
June	6	471 518	59.54	4.09	8 209.0
July	7	188 576	22.41	3.11	16 376.5
Aug.	8	120 334	24.42	3.20	23 062.5
Sep.	9	92 067	23.25	3.15	27 521.0
COHORT 4					
Mar.[a]	2	82 938	60.89	4.11	681.0
Apr.[a]	3	301 119	148.77	5.00	2 374.0
May	4	1 610 755	203.38	5.32	7 346.0
June	5	594 392	70.63	4.26	15 513.5
July	6	105 714	21.33	3.06	22 199.5
Aug.	7	111 654	28.20	3.34	26 658.0
COHORT 5					
June	3	664 899	83.95	4.43	3 960.0
July	4	216 942	25.78	3.25	12 127.5
Aug.	5	12 367	2.49	0.91	18 813.5
Sep.	6	4 911	1.24	0.22	23 272.0

[a] Data not used in the regression analysis

DeLury estimates were obtained for all but cohort 2. This was due to the fact that cohort 2 showed a rather erratic trend in cpue with time. For the other four cohorts some data points were left out of the regression analysis, since evidences of recruitment into the fishery or migration effects were reflected in the cpue estimates.

Final population estimates are given in the following table.

Cohort	Initial population (N_0) in numbers	Catchability coefficient q	r^2
1	954 297	0.00008	0.94
3	2 359 185	0.00010	0.82
4	3 707 255	0.00011	0.89
5	1 121 339	0.00023	0.97

A t-test showed that differences at 95 percent level were not significant between the q values estimated for the different cohorts, implying that each unit of effort is catching the same fraction from each of the cohorts.

No parent stock-recruitment information is available at this time, which might explain differences in initial cohort size (N_0).

6.2 Cohort Analysis

Methods of cohort analysis have been developed by several authors: Fry (1949), Jones (1961), Murphy (1965), Gulland (1965), Tomlinson (1970) and Pope (1972). The basic information required in most of them is a catch vector of numbers of individuals drawn from a given cohort, an estimate of natural mortality rate (M), and an independently estimated initial fishing mortality rate (F).

In this analysis a backward solution to the catch equation given by Murphy (*op. cit.*) has been used). The procedure consists in estimating the exploitation rate E for the last period i with known values of F and M with the expression:

$$ {}_xE_i = \frac{F_i}{F_i + M} (1 - e^{-F_i + M)}) \qquad (6.2.1)$$

Then estimate:

$$ \frac{{}_xE_i}{{}_xR_{i-1}} = {}_xE_{i-1} e^{(F_{i-1} + M)} $$

where ${}_xR_{i-1} = \frac{{}_xC_i}{{}_xC_{i-1}}$, the ratio of catch in number of cohort x in time periods i - 1 and i.

Given that:

$$ {}_xE_{i-1} e^{(F_{i-1} + M)} = \frac{F_{i-1}}{F_{i-1} + M} (e^{(F_{i-1} + M)} - 1) $$

Then F_{i-1} from the right-hand side is estimated iteratively. This value is then used as an initial F-value for time period i - 2, and so on to the last period to be analysed.

Population estimates are obtained for each time period as:

$\frac{x\ C_i}{x\ E_i}$, once the F vector has been obtained.

Data used in the analyses are catch in numbers by cohort as estimated in the previous section. Initial F values for each of the cohorts were independently estimated as F = qf, where q is the corresponding estimate from DeLury analyses and f is the observed fishing effort for the time period considered. An average q value from cohorts 1 and 3 was used to estimate an initial F value for cohort 2.

Population estimates in numbers, and biomass by cohorts and months, and corresponding instantaneous fishing mortality rate estimates are given in Table 3. Figures 13 and 14 show total population in numbers, catch in numbers, effort and cpue. Figures 15 and 16 show total population biomass, catch in weight, effort and cpue.

From the last two figures, it can be seen that maximum population biomass occurs during the months of May and June and that maximum effort and catch in weight occur during June and July, thus dephased one month from the optimum. The cpue in weight does not provide a good index of population abundance. On the contrary cpue in numbers (Figure 8) reflects population decline very well after full recruitment is reached during the month of May.

From Figure 13 it can also be seen that months of maximum effort correspond when population size in numbers is 45.6% and 24.3% of the initial population, while during May population available to the fishery represents 72.6% of the initial population.

Exploitation rates expressed in terms of the number of squid caught during a time period divided by the population at the beginning of that period are given below:

Jan.	Feb.	Mar.	Apr.	May	Jun.	July	Aug.	Sept.
0.001	0.004	0.032	0.096	0.308	0.409	0.372	0.308	0.123

For the period of maximum effort the average exploitation rate is 0.35.

F values averaged over the period of maximum effort and by cohorts are given below:

		Cohort		
1	2	3	4	5
0.28	0.22	0.39	0.60	1.35

6.3 Yield per Recruit Analyses

The theory concerning the estimation of yield per recruit in a fishery was developed among others by Beverton and Holt (1957) and Ricker (1958) and expanded upon by Jones (1957) and Paulik and Gales (1964). Since growth is not always exactly isometric ($\delta \neq 3$) the yield per recruit model given by the latter authors is:

$$Y_w = R\left(\frac{F}{K}\right)W_\infty\, e^{-M(t'_\rho - t_o)}\, e^{-(F + M)\,(t'_\rho - t_\lambda)} \int_a^b X^{\left(\frac{F + M}{K}\right)} (1 - X)^{\delta}\, dt$$

where $X = e^{-K(t - t_o)}$; $a = e^{-K(t_\lambda - t_o)}$; $b = e^{-K(t'_\rho - t_o)}$

Table 3

Cohort analyses estimates

Month	Number of animals		F	Biomass of animals (kg)	
	Catch	Population		Catch	Population
COHORT 1					
JAN	12 226	840 179	0.015	10 053	690 ~~878~~
FEB	28 708	763 840	0.040	43 706	1 162 886
MAR	47 822	677 546	0.076	114 537	1 622 766
APR	67 097	579 543	0.128	227 687	1 966 623
MAY	3 025	470 592	0.006	13 527	2 104 342
JUN	29 760	431 505	0.074	166 345	2 411 921
JUL	157 368	369 758	0.581	1 056 517	2 482 434
AUG	62 198	190 754	0.413	486 262	1 491 310
SEP	30 319	116 509	0.315	268 286	1 030 963
COHORT 2					
FEB	5 901	1 080 420	0.057	4 852	888 428
MAR	44 886	991 687	0.048	68 335	1 509 765
APR	14 833	872 342	0.018	35 526	2 089 315
MAY	51 024	791 026	0.069	173 145	2 684 270
JUN	31 186	681 222	0.049	139 454	3 046 214
JUL	201 040	598 902	0.428	1 123 724	3 347 595
AUG	102 494	360 299	0.350	688 111	2 418 929
COHORT 3					
MAR	84 032	2 688 677	0.033	69 099	2 210 896
APR	418 819	2 401 264	0.200	637 619	3 655 734
MAY	482 315	1 814 891	0.323	1 155 175	4 346 780
JUN	471 518	1 213 069	0.516	1 600 051	4 116 432
JUL	188 576	668 441	0.346	843 524	2 989 061
AUG	120 324	436 332	0.337	672 557	2 438 901
SEP	92 067	287 469	0.404	618 108	1 929 972
COHORT 4					
MAR	82 938	3 788 744	0.023	27 688	1 264 839
APR	301 119	3 417 796	0.096	247 610	2 810 450
MAY	1 610 755	2 865 974	0.871	2 452 247	4 363 318
JUN	594 392	1 107 275	0.811	3 857 861	2 651 995
JUL	105 714	454 250	0.277	358 730	1 541 453
AUG	111 654	317 911	0.453	499 282	1 421 868
COHORT 5					
JUN	664 899	953 044	1.273	221 970	318 165
JUL	216 942	246 356	2.336	178 391	202 578
AUG	12 367	21 986	0.872	18 828	33 472
SEP	4 911	8 985	0.913	11 762	20 322

Table 4

Summation of all cohorts

Month	Total population		Total catch	
	In numbers	Biomass (kg)	In numbers	Biomass (kg)
JAN	9 611 908	1 314 406	48 561	147 044
FEB	8 861 166	3 320 603	73 793	104 233
MAR	8 146 654	6 608 266	260 259	340 618
ABR	8 389 552	10 523 260	679 211	974 407
MAY	6 974 903	13 573 404	1 475 194	1 902 177
JUN	4 386 115	12 544 727	3 170 190	5 559 013
JUL	2 337 707	10 563 121	1 696 567	6 895 828
AUG	1 327 342	7 804 480	685 027	3 448 183
SEP	1 038 585	7 222 269	487 495	2 349 602

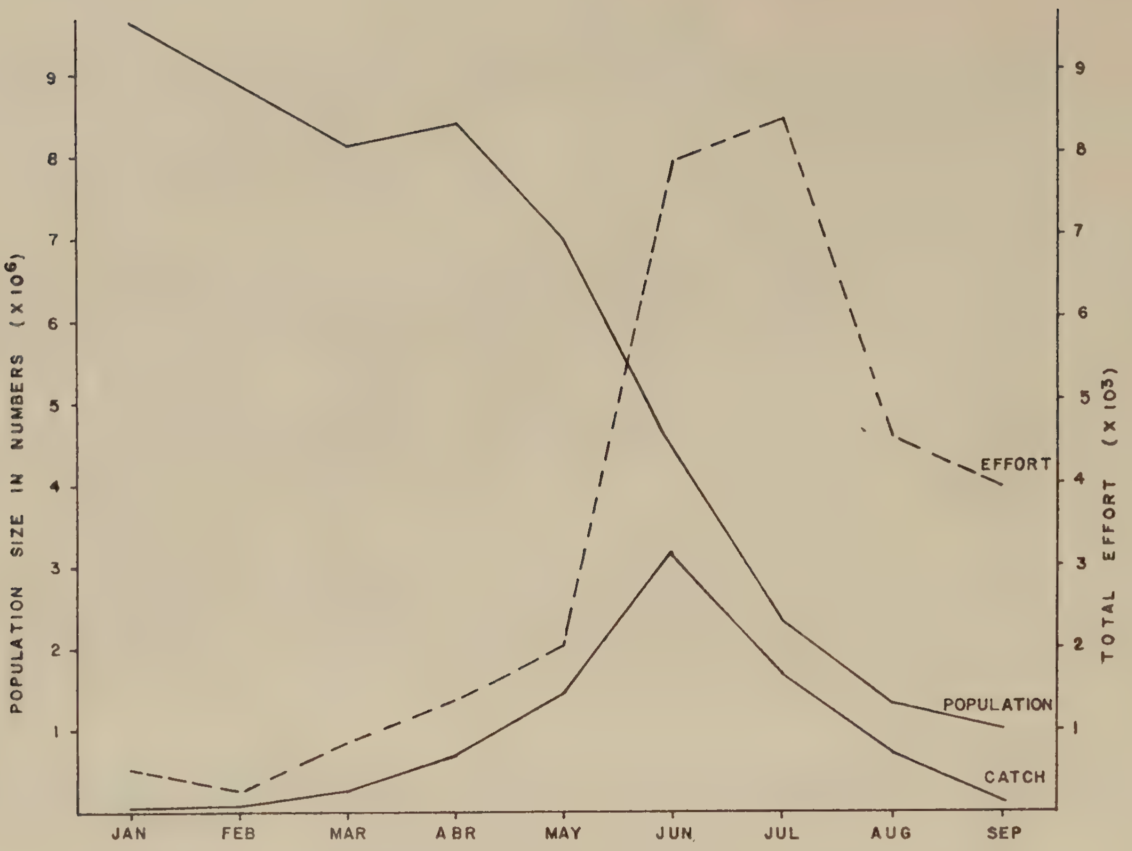


Figure 13 Change in population size and total fishing effort on a seasonal basis

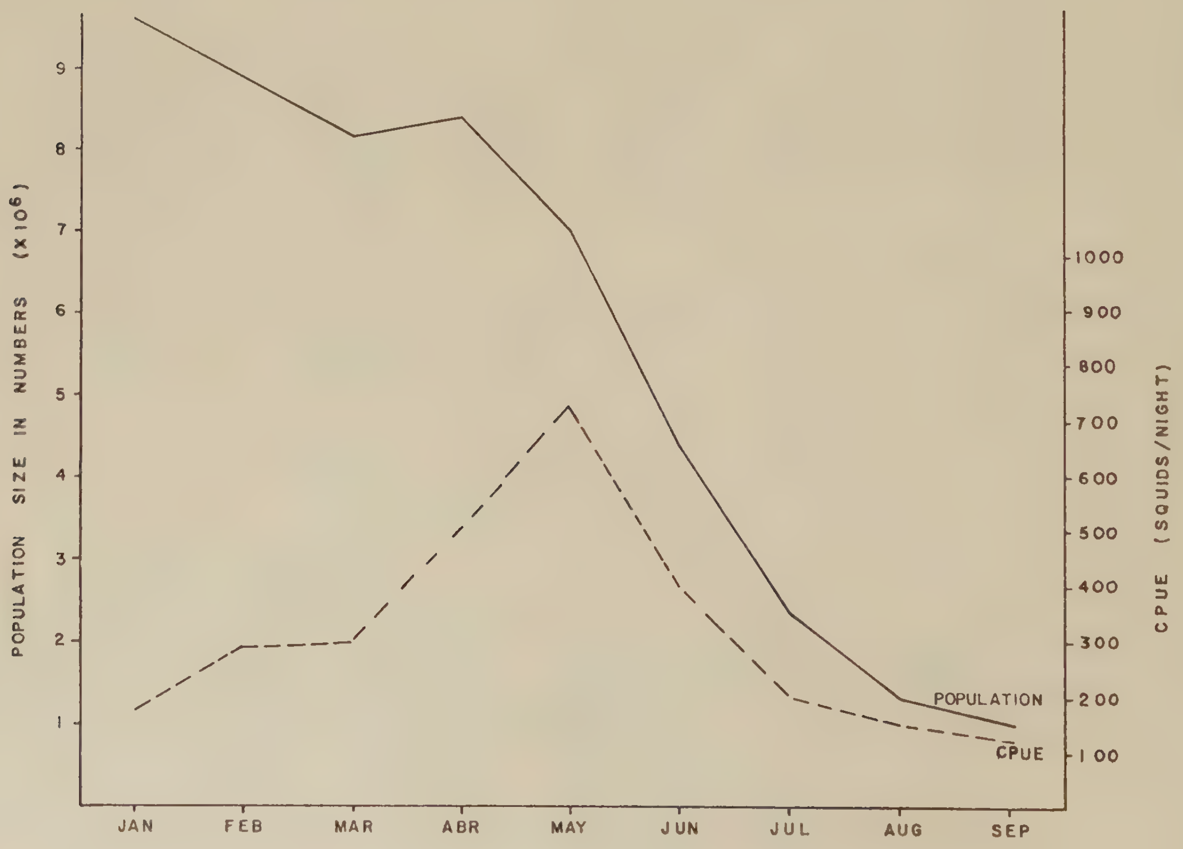


Figure 14 Change in population size and mean catch rate on a seasonal basis

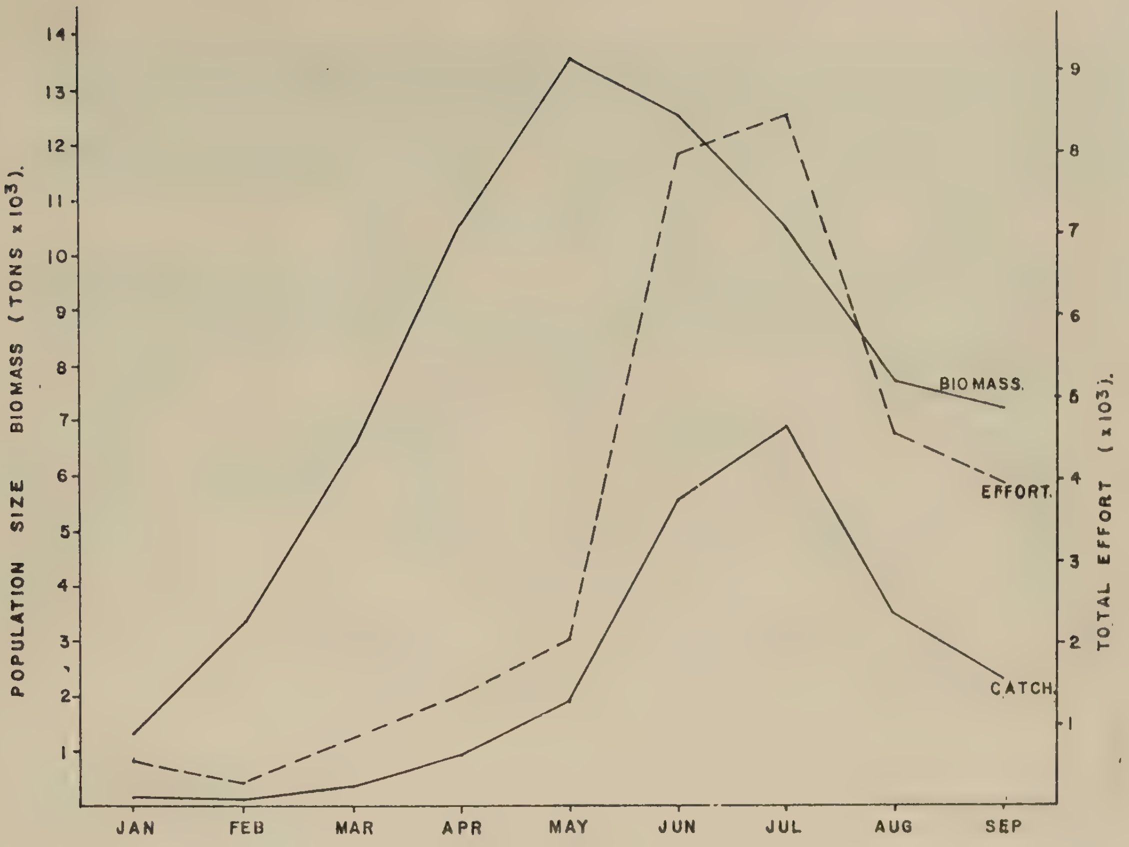


Figure 15 Change in biomass effort and catch on a seasonal basis

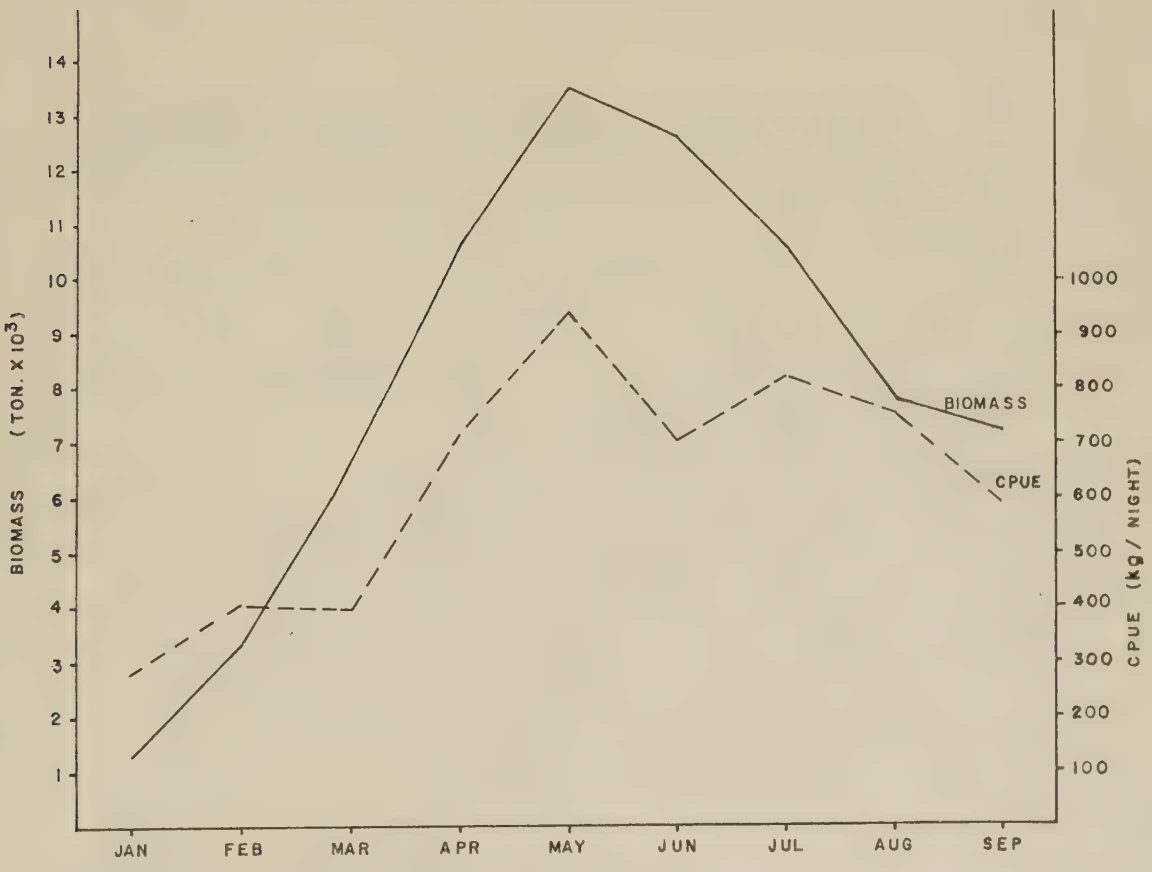


Figure 16 Change in biomass and catch rate on a seasonal basis

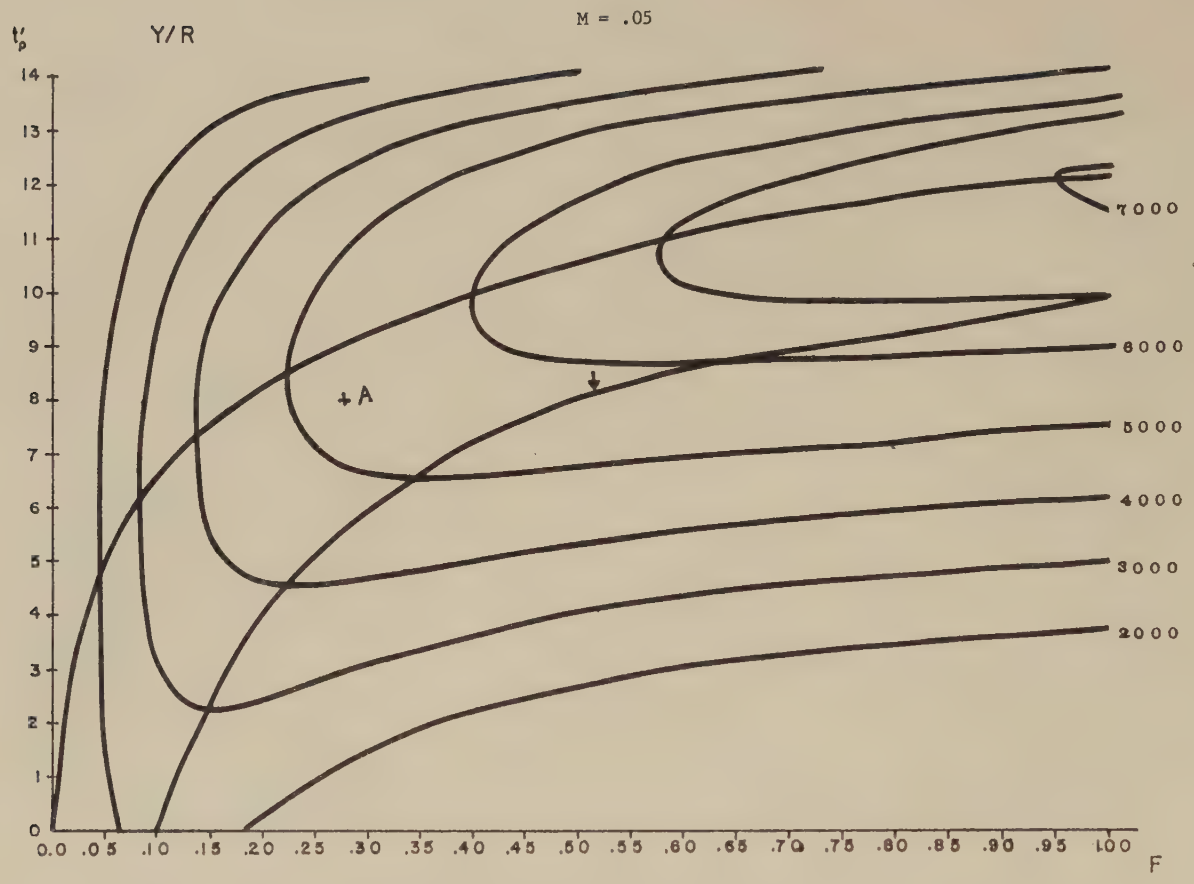


Figure 17 Yield/unit isopleth for cohort 1 (M = 0.05 monthly)

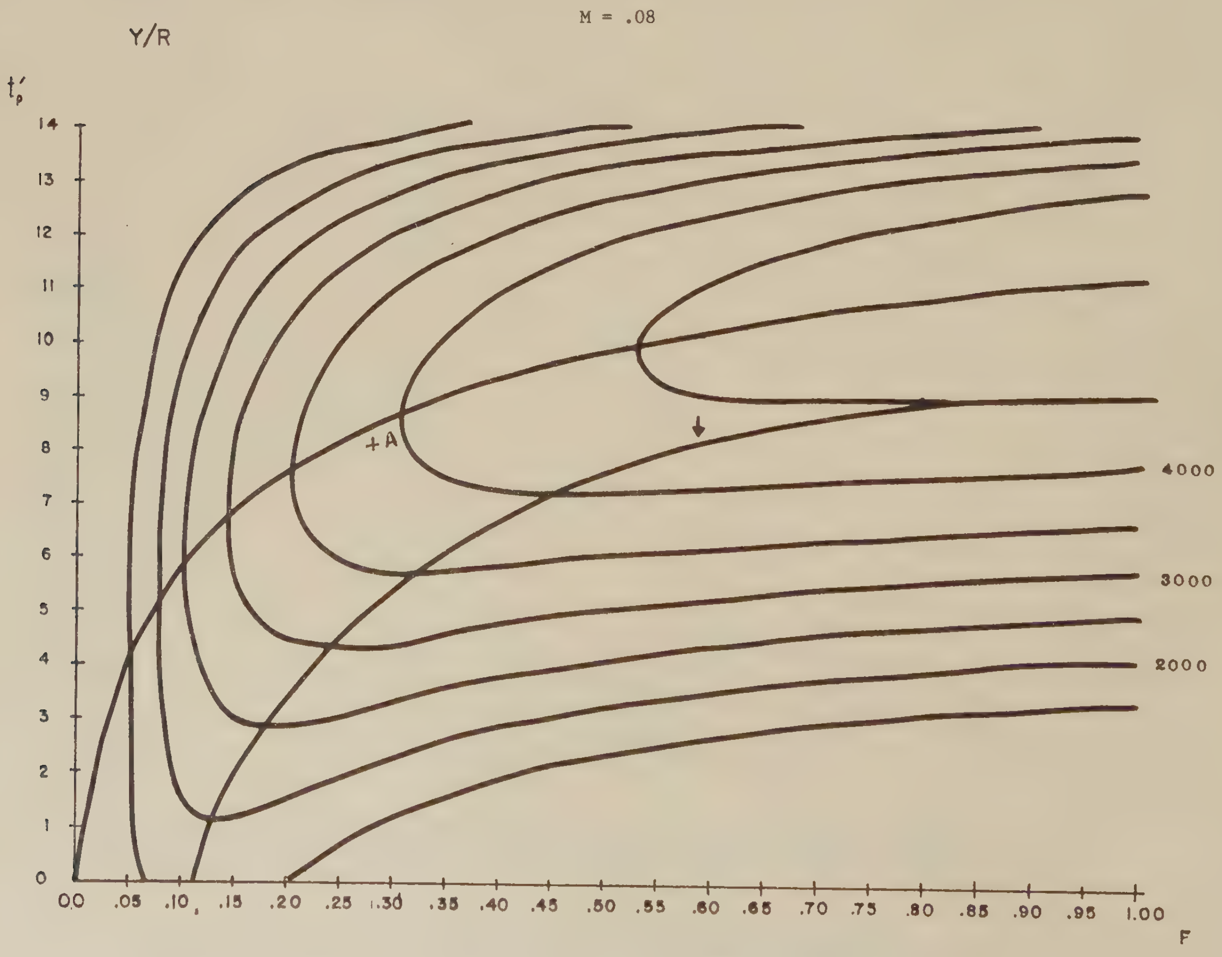


Figure 18 Yield/unit isopleth for cohort 1 (M = 0.08 monthly)

M = .05

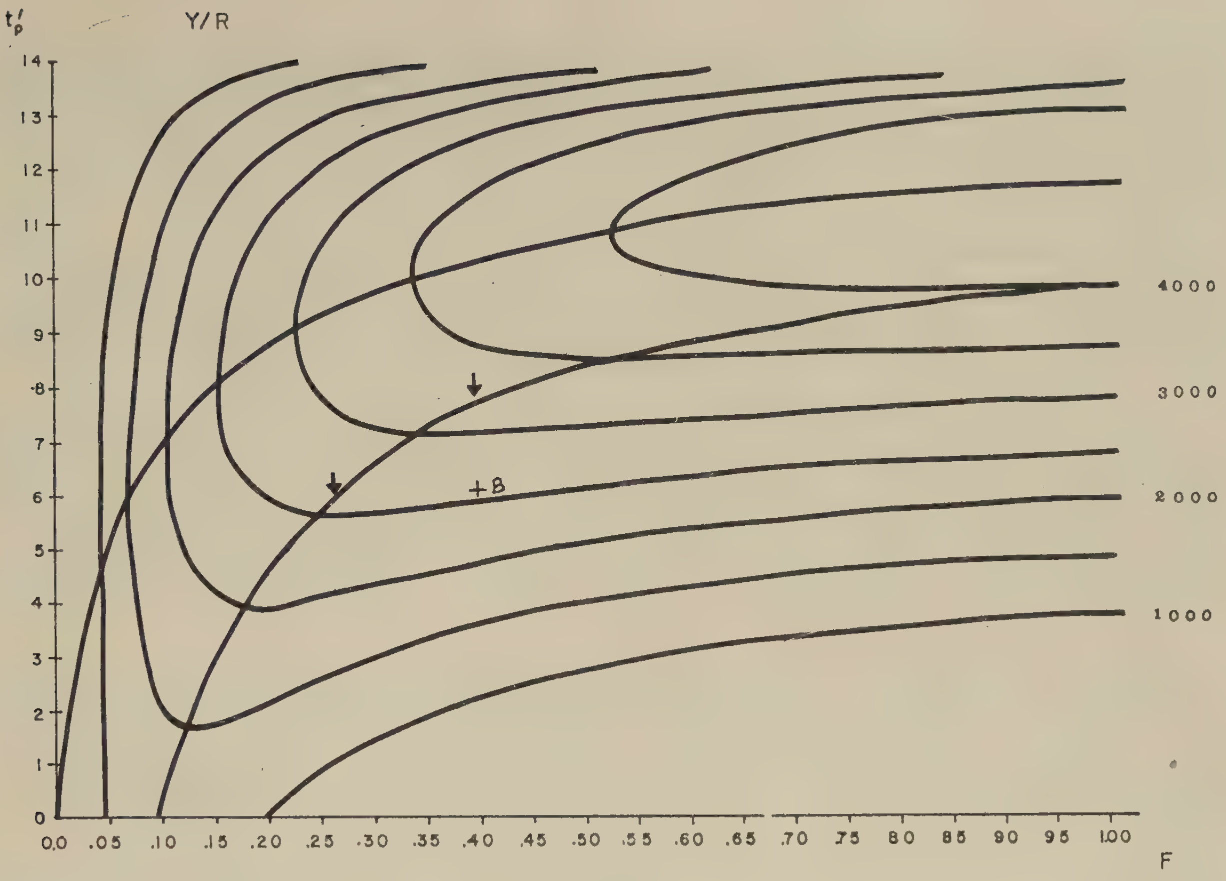


Figure 19 Yield/unit isopleth for cohort 3 (M = 0.05 monthly)

M = .08

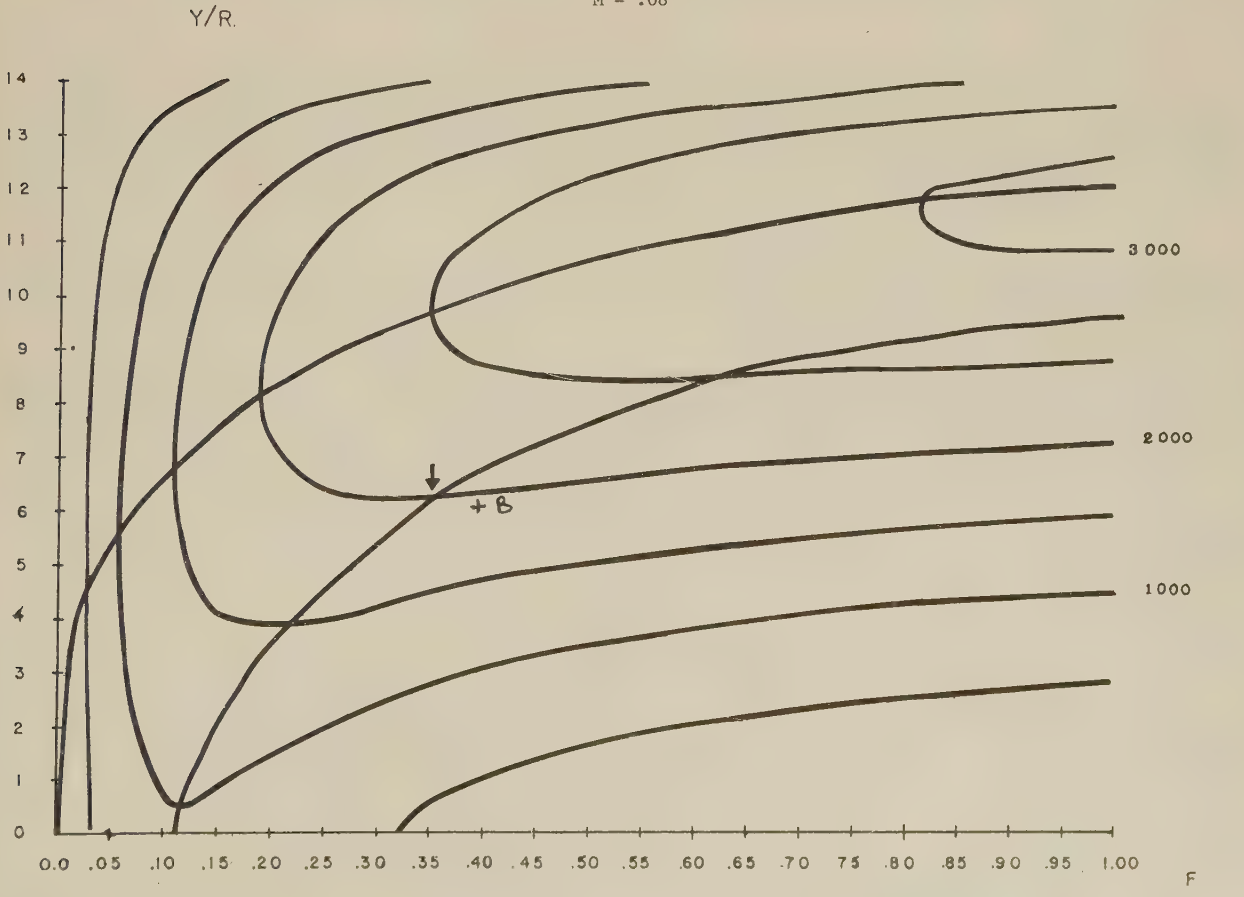


Figure 20 Yield/unit isopleth for cohort 3 (M = 0.08 monthly)

Since the integral in the preceeding equation is in the form of an incomplete Beta function whose integration may be effected by using the polynomial Pn (X) to approximate the function $X^u (1 - X)^v$, the yield Y_w is obtained by evaluating the incomplete Beta function in the lattice points F and t'_ρ. This evaluation has been made by using a computer routine developed by Gales (1963).

Growth parameters for cohorts 1 and 3 and natural mortality rates of 0.05 and 0.08 were used in the analyses. These M values are considered to include the real natural mortality rate for the species within their range. Cohorts 2, 4 and 5 were left out of the analyses since growth parameters valid for their whole life-span were not available. Yield isopleths are given for each of the two other cohorts in Figures 17 to 20.

Cohort 1 recruits at eight months of age in May when all cohorts are fully available to the fishery in the central section of the Gulf of California. The average F value from cohort analyses is F = 0.28. As such, the present position of exploitation of cohort 1 on the isopleth diagrams is given by point A. If the age at full recruitment is kept at eight months, then optimum yield per recruit could be attained at F = 0.52 for M = 0.05, or F = 0.59 for M = 0.08, which means a possible increment of 86% and 110% in F, respectively, to maximize Y/R.

Cohort 3 is recruited to the fishery at age 6m in May, and has an actual average value of F = 0.38. Point B in Figure 20 (M = 0.08) indicates the exploitation position on the isopleths. For M = 0.05, maximum yield per recruit is obtained by either reducing F by 32% to 0.26, or by increasing the age of recruitment to approximately 8 months. For M = 0.08, maximum yield per unit will be obtained by decreasing F from 0.38 to 0.35. Since the fishery is acting on a multicohort stock, management schemes by independent cohorts become impossible. If F has to be increased between 86% and 110% for cohort 1, it would necessarily mean a similar increase in the actual F value for cohort 3 and to manage this cohort for a maximum yield, age of recruitment has to be raised to at least 9 months. This would however require on intensity of fishery which is unlikely to be economically feasible.

7. CONCLUSIONS

The stock of giant squid in the Gulf of California is clearly a single stock with multi-cohort components. These components migrate separately on some occasions, but they usually coincide in time on the fishing grounds. Their recruitment to major fishing grounds occurs around May each year. From May to September the stock presents the highest density, and thus an optimum situation for the fishery.

Different cohorts grow at different rates depending on their birth date, and probably their natural mortality rate is equally different even though it has not been possible to measure this last parameter individually.

Stock assessment analyses indicate that after an explosive fishery development, the stock is now reaching MSY levels; however optimal management schemes are difficult to define unless the fishery is regulated in terms of the least productive cohort.

Since *D. gigas* is a fast-growing and fast-dying species, it is essential to obtain better knowledge of its reproduction potential before advice in terms of fishing levels can be given.

8. REFERENCES

Abramson, N.J. (Comp.), Computer programs for fish stock assessment. FAO Fish Tech.Pap., 1971 (101):148 p.

Allen, K.R., Relation between production and biomass. J.Fish.Res.Board Can., 28(10): 1971 1573-81

Araya, H. and M. Ishii, Information on the fishery and the ecology of the squid, 1974 *Doryteuthis bleekeri* Keferstein, in the Waters of Hokkaido. Bull.Hokkaido reg.Fish.Res.Lab., (40):1-30

Arnold, G.P., Squid: a review of their biology and fisheries. Lab.Leafl.Dir.Fish.Res.G.B.,
1979 (48):37 p.

Baker, A. de C., Observations of squid at the surface in the NE Atlantic. Deep-Sea Res.,
1960 6:206-10

Berry, S.S., A review of the cephalopods of western North America. Bull.US.Bur.Fish.,
1912 30(1910):269-336

Beverton, R.J. and S.J. Holt, On the dynamics of exploited fish populations. Fish.Invest.
1957 Minist.Agric.Fish.Food G.B.(2 Sea Fish.), (19):533 p.

Braaten, D.O., Robustness of the Delury method. MSc. Thesis. University of Washington,
1968 96 p.

Cassie, R.M., Some uses of probability paper in analysis of size frequency distributions.
1954 Aust.J.Mar.Freswat.Res., 5(3):513-22

Clarke, M.R., A review of the systematics and ecology of oceanic squids. Adv.Mar.Biol.,
1966 4:91-300

Delury, D.B., On the estimation of biological populations. Biometrics, 3:145-67
1947

FAO, Yearbook of fishery statistics. Annuaire statistique des pêches. Anuario estadístico
1982 de pesca. Catches and landings. Captures et quantités débarquées. Capturas y
desembarques. Yearb.Fish.Stat./Annu.Stat.Pêches/Anu.Estad.Pesca, vols 32, 34,
36, 38, 40, 42, 44, 46, 48 (covering years 1971-78)

Fields, W.G., The structure, development, food relations, reproduction, and life history
1965 of the squid *Loligo opalescens* Berry. Fish.Bull.Calif.Dept.Fish.Game., (131):
108 p.

Fitch, J.E., Food habits of the jumbo squid, *Dosidicus gigas*. Unpubl. MS
1968

Fridriksson, A., Remarks on the age and growth of the squid. Greinar, Reyk., 2(2):170-4
1943

Fry, F.E.J., Statistics of a lake trout fishery. Biometrics, 5:27-67
1949

Gales, L.E., Incomplete Beta-Function. Program FRG 701. Seattle, University of Washington,
1963 Fisheries Research Institute

García-Tello, P., Utilización de la mandíbula inferior de la jibia *Dosidicus gigas* (D'Orb.)
1965 en el cálculo de su peso total (Mollusca, Cephalopoda, Ommastrephidae).
Rev.Biol.Mar., 12:1-3

Gulland, J.A., Estimation of mortality rates. Annex to report article Fish. Working Group.
1965 ICES, CM. 3:9 p (mimeo)

Harding, J.P., The use of probability paper for the graphical analysis of polimodal
1949 frequency distributions. J.Mar.Biol.Assoc.UK., 28:141-53

Hasselblad, U., Estimation of parameters for a mixture of normal distributions.
1966 Technometrics, 8(3):431-44

Holme, N.A., The biology of *Loligo forbesi* Steenstrup (Mollusca: Cephalopoda) in the
1974 Plymouth area. J.Mar.Biol.Assoc.UK., 54:481-503

Hurley, A.C., Feeding behavior, food consumption, growth, and respiration of the squid
1976 *Loligo opalescens* raised in the laboratory. Fish.Bull.NOAA/NMFS, 74(1):176-82

Jones, R., A much simplified version of the yield equation. Paper presented at Joint
1957 meeting of ICNAF/ICES/FAO, Lisbon. Doc. No. (P21):8p. (mimeo)

__________, The assessment of long-term effects of changes in gear selectivity and
1961 fishing effort. Mar.Res.,Scotl., 1961(2):1-19

México, Departamento de Pesca, Dirección General de Planifación, Informática y estadística.
Anuarios estadísticos pesqueros 1974-80. México, Departemento de Pesca

Murata, M. and M. Ishii, Some information on the ecology of the oceanic squid, *Ommastrephes*
1977 *bartrami* (Lesueur), and *Onychoteuthis borealijaponicus* Okada in the Pacific
Ocean of northeastern Japan. Bull.Hokkaido Reg.Fish.Res.Lab., (42):1-23

Murphy, G.I., A solution of the catch equation. J.Fish.Res.Board Can., 22:191-202
1965

Nesis, K.N., The biology of the giant squid of Peru and Chile, *Dosidicus gigas*.
1970 Oceanology, Wash., 10:108-18

Paulik, G.J. and L.E. Gales, Allometric growth and the Beverton and Holt yield equation.
1964 Trans.Am.Fish.Soc., 93(4):369-81

Phillips, J.B., Two unusual cephalopods taken near Monterey. Calif.Fish Game., 47(4):416-7
1961

Pope, J.G., An investigation of the accuracy of virtual population analysis using cohort
1972 analysis. ICNAF Res.Bull., (9):65-74

Ricker, W.E., Hand book of computation for biological statistics of fish populations.
1958 Bull.Fish.Res.Board Can., (119):300 p.

Robson, D.S., Estimation of the relative fishing power of individual ships. Res.Bull.
1966 ICNAF., (3):5-14

Roper, C.F.E. and R.E. Young, Vertical distribution of pelagic cephalopods. Smithson.
1975 Contrib.Zool., (209):51 p.

Roper, C.F.E., R.E. Young and G.L. Voss, An illustrated key to the families of the order
1969 Teuthoidea (Cephalopoda). Smithson.Contrib.Zool., (13):32 p.

Sato, T., Resultados de la pesca exploratoria para *Dosidicus gigas* (D'Orbigny) frente a
1976 California y México. FAO Inf.Pesca, (170)Supl.1:62-8

Suda, A., Development of fisheries for non conventional species. J.Fish.Res.Board Can.,
1973 30(12)Pt.2:2121-58

Taylor, C.C., Cod growth and temperature. J.Cons.Int.Explor.Mer, 23:366-70
1958

Tomlinson, P.K., A generalization of the Murphy catch equation. J.Fish.Res.Board Can.,
1970 27(4):821-5

Tomlinson, P.K. and N.J. Abramson, Fitting von Bertalanffy growth curve by least squares.
1961 Fish Bull.Calif.Fish Game, (116)

Von Bertalanffy, L., A quantitative theory of organic growth. Hum.Biol., 10(2):181-213
1938

Wormuth, W.S., Morphometry of two species of the squid family Ommastrephidae. Veliger,
1970 13:139-44

Wormuth, J.H., The biogeography and numerical taxonomy of the oegopsid squid family
1976 Ommastrephidae in the Pacific Ocean. Bull.Scripps Inst.Oceanogr.Univ.Calif., (23):90 p.

Yong, M.Y.Y. and R.A. Skillman, A computer program for analysis of polimodal frequency
1975 distributions. Honolulu, Southwest Fisheries Center, NOAA/NMFS, 77p.

APPENDIX 1

PHASE I (Immature)

In females, Nidamental glands are thin and transparent, oviducts not yet formed, eggs not present.

Males have semi-translucent white fibrous testes. Spermatophoric organ is thin and transparent to translucent; spermatophoric sac is empty.

PHASE II (Transition or Maturing)

Sexual organs are well-developed even in shorter individual sizes. In females, the ovary has a granular appearance. Nidamental glands are lightly and creamy-white in colour. Oviducts are scarcely apparent.

In males, testes are creamy-white in colour. The spermatophoric sac can contain a few whitish particles.

PHASE III (Mature)

Female sexual structures have grown considerably in size, full oviducts occupy one third of the mantle cavity. Eggs are strong orange in colour. Nidamental glands are entirely white with an almost proportional size to the oviducts.

In male, the spermatophoric sac is completely full of spermatophores. Testes are white in color and enlarged in size.

PHASE IV (Spawning)

In females, the spiral shaped oviducts are contracted with a few eggs inside. Nidamental glands empty and also contracted, white rosaceous colour.

In males, spermatophoric sac is soft, semitransparent but equal size, it could be some residual spermatophores inside.

Spermatophoric organ contracted against spermatophoric sac. Reabsorption phase beginning.

PHASE V (Spent)

Reproductive organs experiment an apparent reabsorption stage. Nidamental glands almost empty and reduced in size.

SQUID MATURITY SCALES FOR POPULATION ANALYSIS

by

Marcelo Juanicó
Museo Nacional de Historia Natural
Casilla 399
Montevideo, Uruguay

ABSTRACT

This paper is an exhaustive review of the present stage of our knowledge of squid maturity scales, oriented to serve as a guide for population analysis. Twenty-three tables present the different male and female scales now in use and their equivalences. The review also includes a glossary, and describes aspects of the anatomy of the reproductive system, gametogenesis, gonadal development, maturation process, mating, fertilization, spawning and life cycles. Subjects on which there is inadequate information, discussion points and practical problems are pointed out.

RESUME

Ce document présente un examen complet de l'état actuel de nos connaissances sur les échelles de maturité des encornets; son objectif est de servir de guide à l'analyse des populations. Vingt-trois tableaux présentent les différentes sortes d'échelles existentes pour les mâles et les femelles et leurs équivalences. Ce document comporte également un glossaire et des indications sur l'anatomie du système de reproduction, de la gamétogénèse, du développement gonadal, du processus de maturation, de l'accouplement, de la fécondation, de frai et des cycles vitaux. Les questions à propos desquelles on manque d'informations, les points sujets à controverse sont indiqués ainsi que les problèmes pratiques.

RESUMEN

Este artículo es una revisión exhaustiva de los conocimientos actuales sobre escalas de madurez de calamares, orientado a servir como guía en estudios poblacionales. En 23 tablas se presenta los distintos tipos de escalas de madurez existentes para machos y hembras, y sus equivalencias. La revisión también comprende un glosario y aspectos de la anatomía del aparato reproductivo, gametogénesis, desarrollo gonadal, proceso de maduración, cópula, fertilización, desove y ciclos de vida. Son señalados los tópicos sobre los cuales se carece de información suficiente, puntos en discusión, y problemas prácticos.

1. INTRODUCTION

Maturity scales 1/ are widely used in population analyses in fisheries studies. Maturation and age and size at maturity are basic information in the study of reproductive cycles and management models. All squid species studied to date are made up of several populations; the process of sexual maturation is one of the main characteristics where these populations differ. In such a case, maturity scales can be used together with other information in stock discrimination (Juanicó, 1979, 1980).

1/ The concept of "maturity scale" may perhaps be most easily defined as a sequence of observable sets of primary or secondary sexual characteristics that are synchronous in time, and through which the organism in question passes through in sequence during sexual maturation

Information on the squid maturation process is not abundant. Arnold and Williams (1977) refer to it as "scattered, fragmentary and frequently confusing". These authors present an excellent review of decapod reproduction, but do not treat the subject of maturity scales. The present paper is a review of almost all (perhaps all) published information on squid maturity scales and attempts to synthesize our present knowledge of this subject. The bulk of the paper (23 tables) is not a simple transcription of maturity scales but these are selected and commented on in such a way that the review will hopefully be a useful guide to applying maturity scales on other species of squid. Some tables are not literally translated or transcribed in order to standardize terminology.

Squid are not fish and few principles of fish biology apply to these molluscs. On the other hand, their way of life is so different from that of other molluscs (even octopus and cuttlefish) that few analogies can be found in spite of the necessary homologies. Burukovski *et al.* (1977) warn us that "the principles of compiling a squid maturity scale can be used for all squid, but not for cuttlefish and octopuses."

Most of the information on squid is from neritic species. It will not be surprising that when methodical studies on oceanic squid are available, that novelties will be found in their anatomical characteristics, mating and fertilization, maturity processes, etc.

2. ANATOMY OF THE REPRODUCTIVE SYSTEMS

It seems that a single testis or ovary is always found in squid, placed dorsally in the axis of the mantle cavity. Genital ducts, however, can be paired or single.

Females can bear two oviducts (e.g., *Illex, Todarodes*) or only the left one (e.g., *Loligo, Doryteuthis*); nidamental and accessory nidamental glands are always paired. Males only have the left genital duct and spermatophoric complex, with the single known exception of the Oegopsida Lycoteuthidae. In this oceanic family of squid male organs are paired (Voss, 1962).

Detailed anatomical descriptions can be found in Williams (1909), Drew (1919), Oordt (1938), Dillon and Dial (1962), Fields (1965) and Arnold and Williams (1977). Figures 1 and 2 are schematic drawings of the anatomy of males and females. In the following glossary the terms used for reproduction components and maturity scales are defined:

Accessory nidamental glands (ANG): female paired glands of uncertain function (Bloodgood, 1977)

Ampulla: small papilla with ciliate muscular walls that appears as an expansion of the sperm duct (Grieb, 1976; Grieb and Beeman, 1978)

Eggs (Ova): terms used *sensu lato* to denominate ocytes, ovules and fertilized eggs

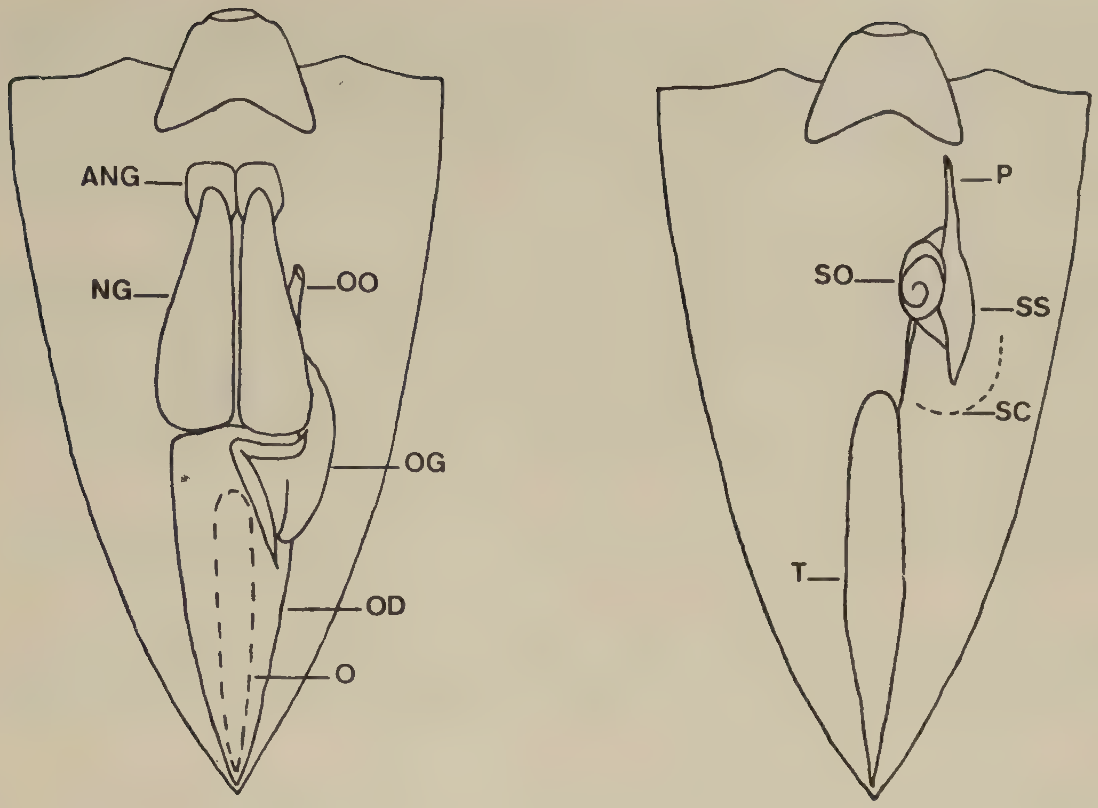
Gonad: testis and ovary; for some authors, ovary + oviduct (Vovk, 1972, 1972a; Durward, Amaratunga and O'Dor, 1978; Table 12)

Hectocotylus: male arm modified for spermatophore transfer by reduction or loss of part of the suckers. In many species this is the lower left arm; in other species it is the lower left or right arm (i.e., *Illex* with a 1/1 left-right proportion. Roper, Lu and Mangold, 1969; Schuldt, 1979). In *Architeuthis* both lower arms are hectocotylized (Kjennerud, 1958). The loss of lower arm suckers during capture may lead to confusing situations in hectocotylus studies (Juanicō, 1979)

Nidamental glands (NG): female paired glands whose secretion is part of the jelly within which eggs are spawned.

Oviduct: membranous duct where the mature eggs are accumulated until spawning. It opens into the mantle cavity through the oviductal gland.

Oviduct meander: term used by Lipinski (1979) referring to the membranous part of oviduct of immature females (Table 9).



FEMALE

MALE

Figure 1 Schematic drawings of squid reproductive systesm. ANG: accessory nidamental glands. NG: nidamental glands. O: ovary. OD: oviduct. OG: oviductal gland. OO: oviduct opening. P: penis. SC: spermatophoric complex. SO: spermatophoric organ. SS: spermatophoric sac. T: testis

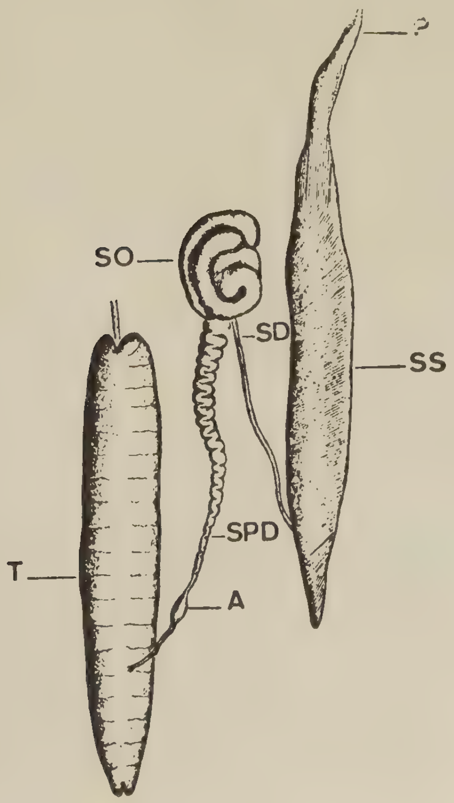


Figure 2 Schematic drawing of male reproductive system. A: ampulla. SD: spermatophoric duct. SPD: sperm duct. Other references as in Figure 1 (modified from Grieb, 1976)

Oviductal gland: terminal glandular part of oviduct, whose secretion is part of the jelly within which the eggs are spawned

Penis: muscular anterior prolongation of the spermatophoric sac which opens into the mantle cavity. Vovk (1972) calls the "spermatophoric duct" the tubular union between the spermatophoric sac and the tip of the penis.

Phase: each of the gametogenesis periods

Sperm duct (spermaduct = vas deferens): ciliary walled duct of male which joins the testis with the spermatophoric organ; it contains the ampulla.

Spermatheca (bursa copulatrix = receptaculum seminis = seminal or sperm receptacle): female rounded protrusion with a central opening, located in the buccal membrane below the mouth. Within it sperm is inactivated and kept for a long time (Oordt, 1938). It is not present in all squid species. See also "spermatophore pad".

Spermatophore (S): described in detail by Drew (1919) and Austin , Lutwak and Mann (1964). In a given species, bigger animals produce bigger spermatophores (Mangold, 1963)

Spermatophore pad: as spermatophores are usually attached onto spermatheca, this structure has been called a "spermatophore pad". LaRoe (1967) points out that other authors used the term to refer to the little protrusion on the mantle wall of female *Lolliguncula*, formed after the attachment of spermatophores.

Spermatophoric complex: anatomical unit formed by the sperm duct, spermatophoric organ, spermatophoric duct, spermatophoric sac and penis (Lipinski, 1979).

Spermatophoric duct (vas efferens): duct through which spermatophores pass from spermatophoric organ to spermatophoric sac. For Vovk (1972) base of the penis; see penis.

Spermatophoric organ (SO)(prostrate gland): organ where spermatophores are formed.

Spermatophoric sac (SS)(Needham's sac): organ where spermatophores are stored. It opens into the mantle cavity through the penis.

Stage of development: each of the periods of the gonad development process

Stage of maturity: each of the periods of the animal sexual maturity process

Testis structure: "the morphological feature which could be seen on the surface of the testis of maturing and mature specimens" (Lipinski, 1979)

3. FEMALES

3.1 Oogenesis

Arnold and Williams (1977) recently made a review of cephalopod oogenesis, so that the only scale described here is that by Knipe and Beeman (1978) (Table 1), chosen because it is concise and clear; some new bibliographical references are however included.

Cowden (1968) described ten oogenesis phases in *Lolliguncula brevis*. Selman and Arnold (1977) argue that Cowden's ten phases overlap, and they recognize only five in oogenesis of *Loligo pealei*. However, the number and type of phases described in different species is very variable, from the three quoted by Bottke (1974) in *Alloteuthis subulata* to the ten defined by Burukovski *et al.* (1977) for *Sthenoteuthis pteropus* as "clearly distinguished." A study of the various scales suggests that the differences among them are due to the techniques or criteria applied by each author, and not to actual differences among the oogenesis processes of each squid species. Table 2 shows the approximate equivalences among oocytes scales; the possible equivalence of Cowden's (1968) scale could not however be established.

Oogonia have been described only by Takahashi and Yahata (1973), Knipe and Beeman (1978) and Schuldt (1979); their descriptions do not fully coincide. Burukovski and Vovk (1974) and Burukovski *et al.* (1977) refer to the presence of oogonia-like cells, but they think that these cells also could consist of the future follicular epithelium.

3.2 Development of the Female Gonad

The ovary is composed of a stroma and groups of cells clustered about ramifying blood vessels, forming structures called "nests". In the nests, almost all (or all) oocyte phases are found, up to the most advanced phase of the corresponding gonadal development stage; in each "nest" of a spawning female only early oocytes are lacking (or are poorly represented). Thus, the number of cell types and the cell size range both increase as the gonad matures (Figure 3).

Scales of gonad development were established based on:

(a) the phase of the most advanced oocytes and the size and appearance of the gonad (Table 3), and

(b) the diversity of cell types and sizes (Table 13).

These scales must not be confused with maturity scales, which also take into account other structures of the reproductive system.

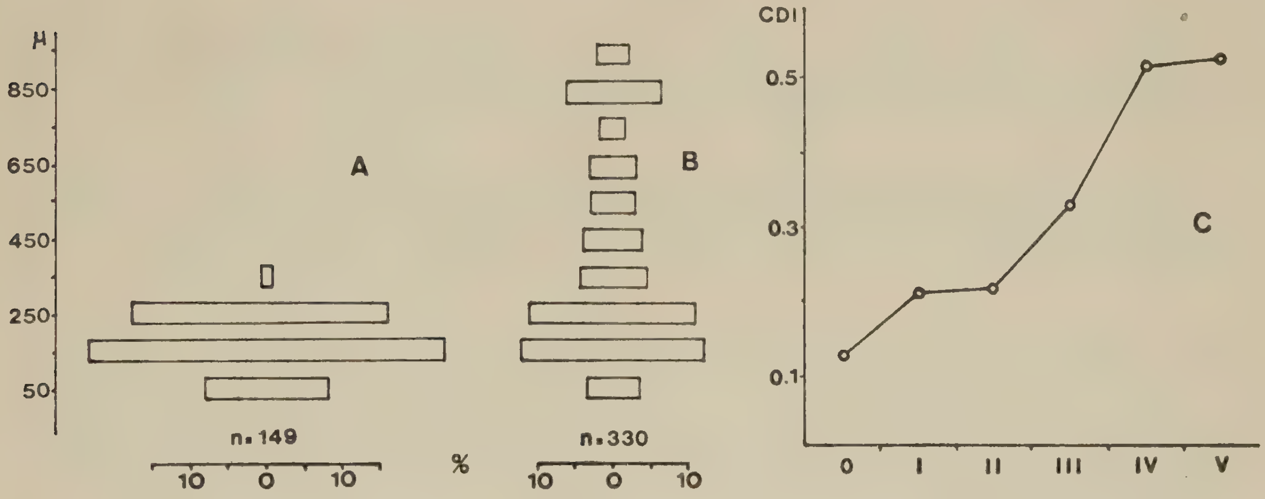


Figure 3 Cellular structure of *Illex argentinus* ovary. A: size cellular distribution in an ovary in stage I; B: ibidem in an ovary in stage V; C: Cellular Diversity Index (CDI) in each ovary development stage.
CDI = c - (1/ Log_e N)where c = number of cellular types, and N = total number of cells (Schuldt, 1979)

3.3 Female Maturity Scales

Immature/mature scales: The simplest scales are those which only distinguish immature and mature females. Authors often define only the characteristics of the mature females, being implicit that the immature females do not have them. Table 4 shows several of those definitions. These scales are too simple for any serious population study.

Immature/maturing/mature scales: In these scales the mature stage is defined by the presence of mature eggs (amber colour, without reticular system) independently of their quantity, and one or two maturing stages are also recognized.

The parameters considered in constructing these scales vary widely with the authors. Mangold (1963) (Table 5) uses the relative size of the eggs; Vovk (1972), makes a complete analysis of almost all the structures of the reproductive system; Whitaker (1978) (Table 6) strengthens the importance of the colour of the ANG; Juanicõ (1979) (Table 7) makes use of Vovk's (op. cit.) criteria which can be applied to material in fixed or poor condition and which are valid in more than one species.

Vovk's (op. cit.) scale was transcribed taking into consideration some of the observations on oogenesis by Burukovski and Vovk (1974). Burukovski *et al.* (1977) (Table 11) made some other modifications and added another stage; this latter scale is the one reproduced in the present review. The scale by Holme (1974) for *Loligo forbesi* is based mainly on the relative size of the ovary and the NG; unfortunately the descriptions are insufficient and subjective. Kashiwada and Recksiek (1978) employ for *Loligo opalescens* a simplification of Vovk's (1972) scale, so that it is not included here.

Scales which distinguish mature and fully mature stages: In this case the number of mature eggs let us distinguish females ready to spawn from those which are not. Females with mature eggs may be mature but not ready to spawn. Females with many mature eggs are fully-mature and ready to spawn. A typical example is Hamabe and Shimizu's (1966) scale for *Todarodes pacificus* (Table 8). The one used by Nesis (1970) for *Dosidicus gigas* is very similar, so it is not described here.

Lipinski's (1979) (Table 9) scale can be included in this category. He developed a scale which could be applied to all squid after considering the common characteristics of 17 species (Myopsida and Oegopsida) and removing the differences. He called it the "Universal Maturity Scale."

Scales which include morphometric or gravimetric relationships: These relationships refer to the size and weight of the ovary and/or NG, as compared to other organs or to the body. As these relationships generally are different in each species, this kind of scale cannot be extrapolated to other species.

Hayashi (1970) (Table 10) only makes use of the relationship between ovary weight and oviduct weight, when constructing an immature/mature scale for *Todarodes pacificus*.

The other three transcribed scales (Tables 11, 12 and 13) use more than one index, and include considerations of the histological and macroscopic development of the gonad, NG and other organs, thus providing a genuine description of the maturation process. Burukovski *et al.* (1977) (Table 11) divide the mature stage into three substages which are a detailed description of the pre-spawning period.

Barragãn (1969) developed for *Lollinguncula brevis* a scale similar to that of Duward, Amaratunga and O'Dor (1978) (Table 13) but he does not state which index was used, and the suitable bibliographic reference is lacking. This scale is not presented here.

The degree of oviduct filling of Tinbergen and Verwey (1945): These authors studied *Loligo vulgaris* off the coasts of Holland, describing the maturation process, but their description is not a scale by itself. In parallel, they classified females according to the amount (relative to the size of each female) of mature eggs in the oviduct: many (full) - moderate - few - none (empty).

This division of the mature stage into three substages was described in 1945 and used successfully as will be seen in the following examples. Curiously, in spite of Tinbergen and Verwey's paper being continuously quoted since then, its three substages were not used again up until 1977 in Burukovski's scale (Table 11).

Equivalences among the different scales: A table of approximate equivalences (Table 14) was made, based on a detailed study of the various scales. This table will be useful in allowing quick comparisons among the different papers on the subject.

3.4 The Use of ANG in Maturity Scales

Before using ANG as indicators of maturity, it should be checked that a real correlation between these glands and the maturity process exists in the species and population under study.

The development of the ANG as an indication of maturity has been used by some authors. Drew (1911) mentions them in *Loligo pealei* noting that "females that are nearly ready to deposit eggs have the NG considerably swollen and the ANG are highly coloured bright red... Frequently the borders of the ANG, which are very red at this time of mating may be seen through the semi-transparent mantle and thus form a further indication that the eggs are nearly ready to be deposited... The ANG are very active during this period and secrete a viscid material. What the special function of this secretion is has not been determined. It would seem from the position and activity that the secretions from both sets of glands (ANG and NG) must be mixed as they are poured out."

Cohen (1976) includes ANG length in her parameters to recognize spent females. Whitaker (1978) uses their colour as an important element in his maturity scale (Table 6). Burukovski and Vovk (1974) also make use of ANG colour and size, but Burukovski *et al.* (1977) abandon this indicator.

The original idea that the ANG assist the NG in the secretion of egg masses was discussed by Buchner (1965), who found dense populations of bacteria in the ANG of some squid. This fact was confirmed and discussed by Bloodgood (1977). There are two reasons to question the use of ANG in maturity scales:

(1) The real function of these glands is not known. It is possible that they are are not directly related to reproduction; many squid have luminescent ANG, but some species have other luminescent organs which have been considered important in sex attraction (Young, 1975).

(2) The red colour of ANG during maturity is due to the presence of bacteria in their tubules. Although in the few well studied species there is a clear correlation between maturity and redness, the mechanism by which bacteria invade ANG is not known.

3.5 Presence of Spermatophores on Females as a Mating, Maturity or Spawning Indicator

Another of the important points in determining the state of sexual maturity of female squid is to determine if mating took place, and if it did, when and where. Two kinds of mating have been described in squid: head-to-head and head-to-mantle (Drew, 1911)

In head-to-head mating, the male transfers the S by means of the hectocotylus to the buccal membrane, on the female spermatheca. According to Drew (op. cit.) in *Loligo pealei* S lose their cases when they leave the penis, but it seems probable that the sperm do not all escape for two or more days. Sperm is accumulated in the spermatheca where it could be preserved for several weeks. The expelled S, without their cases, rest some time fixed to the spermatheca; staining the buccal area with methylene blue greatly facilitates the observation of spermatheca, sperm and S remain. Some squid species only perform this type of mating, e.g., *Loligo vulgaris* (Tinbergen and Verwey, 1945; Mangold, 1963), *Loligo edulis budo* (Ikehara *et al.*, 1977), *Todarodes pacificus* (Hamabe and Shimizu, 1959; Katoh, 1959; Araya, 1976), *Todarodes sagittatus* (Clarke, 1966), *Dosidicus gigas* (Nesis, 1970). The presence of sperm in the spermatheca proves that mating has occurred; the presence of S remains on the spermatheca and establishes that mating has been relatively recent.

The empty cases of S generally are swallowed by the female, and they persist about 5-10 hours in the stomach without being completely digested (Hamabe and Shimizu, 1959). These authors could estimate accurately enough the most frequent mating period of *Todarodes pacificus*, through the study of the female's stomach contents. Similar observations in *Dosidicus gigas* are quoted by Nesis (1970).

In head-to-mantle mating, the deposition of S is on the internal mantle wall, generally near the left oviduct opening, although it can also be on the right side and on the gills or visceral mass. Durward *et al.* (1979) mention al exceptional *Illex illecebrosus* female which had S almost filling the mantle cavity and even on the outer side. Some squid species do not deposit spermatheca on the buccal membrane and only perform this second kind of mating; i.e., species of the genus *Lolliguncula* (Steenstrup, 1880; Voss, 1956; LaRoe, 1967; Juanicõ, 1979; Brakoniecki, 1980), species of the genus *Illex* (Mangold, 1963; Hamabe, Sato and Kawakami, 1974; Durward *et al.*, 1979; Juanicõ, unpublished observations). In these cases, it seems that the S do not rupture immediately so that there is a delay between mating and fertilization (Mangold, op. cit.; Durward *et al.*, op. cit.) but this is not confirmed. In *Lolliguncula brevis* a small knob is formed on the mantle wall where the S are fixed; LaRoe (op. cit.) argues that this knob has no function and it is "possibly the result of physical irritation." In the Oegopsida *Abralia verayi* S are implanted on a small elevation of the inner dorsal mantle wall, behind the nuchal cartilage (Steenstrup, 1880; Berry, 1926; Clarke, 1966).

In the species which only perform this kind of mating, the presence of S in the female indicates that mating took place, but there is still not enough information to know how long before capture it occurred, since to date it has not been established how long and in what quality the S can persist attached to the female.

Squid which perform both types of mating: In these cases head-to-head copulation takes place before arriving on the spawning area, and females can store sperm in the spermatheca for later fertilization; head-to-mantle mating is prevalent only just before or during spawning. This is the case for *Loligo pealei* (Drew, 1911; Arnold, 1962; Vovk, 1972, 1972a; Arnold *et al.*, 1974; Burukovski and Vovk, 1974; Mesnil, 1977; Whitaker, 1978), *Loligo opalescens* (McGowan, 1954; Fields, 1965), *Loligo brasiliensis* (Castellanos, 1967; Juanicõ, 1979), *Doryteuthis pleiy* (LaRoe, 1967; Waller and Wicklund, 1968; Whitaker, op. cit.; Juanicõ, op. cit.) and *Sepioteuthis sepioidea* (Arnold, 1965; Arnold and Williams, 1977). Several authors specified which was the most frequent mating type found in isolated samples of a species; the differences found depend on when the samples were caught as to the most frequent mating type noted at that moment. In many cases, S remains were found in both the spermatheca and the mantle cavity.

In these species, the presence of S in the females proves that mating took place, and their location indicates whether it is close to the time for spawning or not.

Other modes of depositing S have been described in the holopelagic Oegopsida *Chaunoteuthis mollis* and *Leachia pacifica*. In *C. mollis* S are put in the ventral outer surface of the mantle, in one or two longitudinal strips. The method of copulation is unknown, but it is hypothesized that "the male cuts the skin of the female with his beak and places the S along the cut. Then the edges of the wound close and the S remain firmly fixed in the tissues of the female" (Torchio, 1967, 1976; Nesis, 1970a). The mating type of *L. pacifica* is also unknown, but Young (1975) describes a female in which "discharged S, embedded in the dorsal surface of the head and mantle indicated that mating had occurred."

Immature females of some species do mate and carry S. Hamabe (1964) mentions that of a *Todarodes pacificus* female group carrying S, 70-90 percent were immature; females would keep sperm in the spermatheca while maturation was completed. In other cases, only fully mature females carry S, and they are not found in immature or slightly advanced females; i.e., *Loligo edulis budo* (Ikehara *et al.*, 1977). Between these extremes a gradient of species can be found, in which different percentages of immature females can carry S.

As can be seen, the squid reproductive process includes two steps: copulation and spawning. In many species there is a lag between these steps; this pattern stresses the differences between many squid and most of the commercial fish.

4. MALES

4.1 Spermatogenesis and Gonad Development

There are two squid species in which spermatogenesis is well known, and both differ in synchronization of cellular maturation.

Squid spermatogenesis has been poorly studied; the first information on it are eight lines on *Loligo forbesi* by Franzén (1955). Other brief references on *Loligo pealei* are given by Arnold and Williams (1977). Recently, Grieb (1976) and Schuldt (1979) have added some interesting information on *Loligo opalescens* and *Illex argentinus,* respectively; Grieb and Beeman (1978) published an abridged version of Grieb's (op. cit.) paper. None of these authors make a proper spermatogenesis scale, but Grieb (op. cit.) describes different types of spermatocytes and spermatids.

Grieb (op. cit.) and Grieb and Beeman (op. cit.) studied males of *Loligo opalescens* spawning population, and divided them into three categories:

(1) Seminiferous tubules with secondary spermatocytes; lesser frequency of maturing and mature spermatids. Some S in SS; animals almost ready to spawn.

(2) Maturing and mature spermatids represent the preponderant gametogenic phases; secondary spermatocytes are rarely found. SS filled with S; animals ready to spawn.

(3) Only mature or very later maturing spermatids within the seminiferous tubules. SS with very few S; spent animals (see Table 23).

These authors add that "the cell divisions leading to the production of mature sperm in individual *Loligo opalescens* are almost synchronous."

Schuldt (op. cit.) studied *Illex argentinus* and also divided males into three groups, but these do not correspond to Grieb's groups.

(1) ML 7-9 cm; immature animals. Intense gonial proliferation, with big spermatogonias and some little ones.

(2) ML 17 cm; maturing animals. In the base of the tubules are gonial cells in different phases, second order spermatocytes predominate, and some spermatids.

(3) ML greater than 22 cm; mature animals with S. Same as in (2) above, completing the spermatogenesis.

In *Illex argentinus* the whole cellular series is found in the tubules of mature animals so that the process of spermatogenesis is asynchronous.

These differences in the spermatogenesis of *L. opalescens* and *I. argentinus* merit a more detailed study.

4.2 Male Maturity Scales

Immature/mature scales: These scales have been used by several authors but they are not alike (Table 15). They can be placed in two groups:

(a) scales in which "mature" is a male containing S in SS, and

(b) scales in which it is considered whether the S are underdeveloped or fully developed, and "mature" males are defined as those with fully developed S.

These types of scales are too simple for population studies.

Scales with one maturing stage: The maturing stage can be defined only by the presence of few S in the SS (Nesis, 1970; Schuldt, 1979). Other authors completed this definition with observations on the sperm duct (Mangold, 1963), or the S and testis size (Kashiwada and Recksiek, 1978; Juanicó, 1979) (Table 16, A). Araya and Ishii (1974) made a scale for *Doryteuthis bleekeri* in which the maturing stage is not defined by the presence of few S in the SS, but by the opacity of the sperm duct which is transparent in immature animals (Table 16, B).

Scales with two maturing stages: In these scales various aspects of the reproductive system are combined to divide up the maturing stage. Mercer (1973, 1975) made one of these scales for *Illex illecebrosus*, and Whitaker (1978) (Table 17) one for *Loligo pealei* and *Doryteuthis pleiy*. Lipinski (1979) made a "Universal Scale" (Table 18) based on data of 17 squid species; essentially, it is like that of Mercer (op. cit.) but more detailed.

Holme (1974) developed a four maturing stages scale for *Loligo forbesi*, but the definitions of each stage are subjective and not clear.

Scales which distinguish between mature and fully mature: Vovk (1972) developed a scale of this type for *Loligo pealei* (Table 19).

Hayashi's gravimetric scale: Hayashi (1970) developed an immature/mature scale for *Todarodes pacificus* males (as for females) based on the relative weight of the testis and SS (Table 20).

The SS filling degree of Tinbergen and Verwey (1945): As in the "oviductal filling degree" of females, these authors classified *Loligo vulgaris* males according to the degree of SS filling: full - half full - filled 1/4 - almost empty - empty, stating that "these designations do not relate to the absolute amount of the contents but rather, to the relative amount; that is, they take the size of the animal into account."

This kind of scale has not been used again since its publication in 1945. A similar but simpler analysis was done by Hamabe and Shimizu (1966) in *Todarodes pacificus*.

Equivalences among different scales: A detailed study of the different scales allow the construction of a table of approximate equivalences among them (Table 21).

4.3 Relative Hectocotylation as a Maturity Indicator

Schuldt (1979) studying *I. argentinus* analysed the relationships among the percentage of hectocotylation (percentage of the hectocotylus length with reduced suckers), squid size, and SO size, finding a positive correlation. In *I. argentinus* S formation starts when SO reaches 1.5-3 cm. Schuldt concludes that "a relative hectocotylation greater than 45 percent prooves the existence of mature animals."

This is a useful technique when working with commercially caught squid, because the maturity stage can be determined externally without damaging the animals. The correlation between relative hectocotylation and maturity must be different in each species, so that it is necessary to determine this in each case.

5. DARKENING OF BEAKS AS A MATURITY INDICATOR

Clarke (1962) describes the beaks of several cephalopod species and the possible value in their study. In some species the initiation and spread of darkening of the beaks coincides with the onset of sexual maturity (presence of S in males and expansion of NG in females, for Clarke). Beaks can also be used for the determination of systematics, and its size is correlated with animal length.

After research on the species in a given area, the analysis of beaks from stomach contents of squid predators or marine sediments, would provide extra information on these species, especially on the length and maturity stage of eaten and dead specimens (Clarke, MacLeod and Paliza, 1976).

6. SPENT STAGE AND THE LIFE CYCLES

The life cycle of most squid species is unknown. In two of the best known species (*Todarodes pacificus* and *Loligo opalescens*) both males and females die soon after spawning (Hamabe, 1963; Hayashi, 1971; Yasui, 1975; McGowan, 1954; Fields, 1965; Frey and Rechsiek, 1978). This led to the assumption that other squid species also spawn only once, and they were thus considered terminal spawners (Arnold and Williams, 1977; Arnold, 1979). However, there is strong evidence that some species may spawn more than once.

6.1 Spent Animals

There are few observations on spent squid, due to the difficulties of catching animals at this stage. Some authors have never caught a spent squid and named it "the hypothetical stage" (i.e., Lipinski, 1979). Three hypotheses could explain the low sampling frequency of spent animals:

(1) squid die soon after spawning,

(2) squid swim out of the fishing area after spawning, or

(3) spent squid quickly recover from spawning and return to a maturing stage.

Probably each of the three cases occur in different species. Juanicó (1979) and Schuldt (1979) suggested that the males of some species would continue producing spermatozoa and S once maturity is reached; the spent stage would not exist in these males.

Tables 22 and 23 contain some definitions of female and male spent stages, respectively. There are some discrepancies between authors, but these are surely due to terminology (for example, NG size refers either to length or to volume).

6.2 Species with only One Spawning

In these species the animals die soon after spawning. In *Loligo opalescens* and *Todarodes pacificus*, dead or exhausted specimens are often found in the spawning areas. Histological studies on *L. opalescens* spermatogenesis and oogenesis show that spent specimens do not have germinal cells which would allow another spawning (Grieb, 1976; Grieb and Beeman, 1978; Knipe and Beeman, 1978). A detailed description of the post-spawning death process of *Todarodes pacificus* has been provided by Hamabe (1963) and Hayashi (1971).

6.3 Species which Should Have More than One Spawning

Roper (1965) observed a *Doryteuthis plei* female spawning in an aquarium, which four nights later spawned again, and lived one more week in good condition. LaRoe (1967) studies the general biology of *D. plei* and made some observations in aquaria. He concluded that "they possibly live up to three years, and probably spawn every six months; each individual may undergo multiple spawning during each spawning season." From a research submersible, Waller and Wicklund (1968) observed the mating and spawning of this species, stating that "we saw no evidence of mortality after spawning." Also Cohen (1976) argues that *D. plei* "probably do not die immediately after spawning." Juanicó (1979) agrees with these opinions on *D. plei*, partially based on the finding of mature and spent females with stomach contents similar to those of maturing animals. Hixon (personal communication) is of the opinion that *D. plei* would die after a long spawning period (of several months) during which there would be several discrete spawnings to exhaustion.

A process similar to that proposed by Hixon for *D. plei* would occur in *Loligo vulgaris*. Tinbergen and Verwey (1945) referring to spent females argue that "a rather large percentage thereof have newly deposited spermatophores on the spermatheca, which indicates that egg-laying often is followed by copulation... the animals apparently produce several batches of eggs, the first one being the largest." Mangold (1963) is of the opinion that *L. vulgaris* have more than one spawning period.

Referring to other species, e.g., *Illex illecebrosus*, there are several authors who propose or assume a nearly absolute post-spawning mortality (Squires, 1967; Nesis, 1970; Mesnil, 1977). However, Amaratunga, Roberge and Wood (1978) in a recent publication argue that "the life cycle of *I. Illecebrosus* is still largely a matter of conjecture...." A similar situation is the case with respect to our knowledge on *Loligo pealei*, *Loligo forbesi*, *Loligo brasiliensis*, *Doryteuthis bleekeri*, *Sepioteuthis arctipinnis* (Rao, 1954), *Illex coindeti*, *Illex argentinus*, *Dosidicus gigas*, etc.

There is little information on this aspect of squid biology, and we can only make a working hypothesis for most species. This is one of the most important problems to solve for correct evaluation and management of any squid resources.

7. FACTORS AFFECTING SQUID SEXUAL MATURATION

"Until now, it has not been possible to describe unequivocally any general external factor that would induce sexual maturation in cephalopods" (Mangold and Froesch, 1977).

Temperature variation, photoperiod variation and starvation have been quoted as possible external factors affecting squid maturation and egg laying (Mangold *et al.*, 1975; Rowe and Mangold, 1975; Arnold and Williams, 1977). In *Illex illecebrosus* Mercer (1973, 1975) observes that as the summer-autumn season develops, the size at which males mature lessens. He associates this quickening of maturation with the decrease in day-length. Whitaker (1978) says that apparently the big males of *Doryteuthis plei* are mature year-round, and that seasonality occurs only with the smaller specimens. Mangold and Froesch (1977) studying *Octopus vulgaris*, suggest that the gonad develops independently of external factors.

8. TWO EXAMPLES OF THE APPLICATION OF MATURITY SCALES

8.1 First Example

Tinbergen and Verwey (1945) studied *Loligo vulgaris* biology off Holland based on 12 000 individuals. This species is present year-round, but abundant from April to August.

During summer, the degree of filling of SS in the population dropped; this was interpreted as S deposition (due to mating activity) being greater than S production. From May to early August the degree of the filling of the oviduct dropped also; this was interpreted as meaning that lots of egg-laying was greater than their production.

The authors computed a "mating ratio" (females with S remain on the spermatheca/ females with spermatheca filled with sperm). A filled spermatheca proves that the female mated; however, not all the females with filled spermathecas carry S remains, because S are lost after a while. This ratio was maximum from late May to July, showing that during that period the maximum mating activity took place.

Spent specimens were also found in the area from May to August. All of these observations allowed the precise determination of the spawning area and time off the Dutch coast.

8.2 Second Example

Juanicó (1979, 1980) studied the biology of *Loligo brasiliensis* in the southwestern Atlantic between Rio de Janeiro and Mar del Plata, based on 2 500 individuals sampled in five geographic localities latitudinally distributed.

Through the use of maturity scales (Tables 7 and 16), the size (mantle length) at which 50 percent of the individuals of each sample reached the maturing stage was calculated. This allowed the detection of differences in the sexual maturity process among samples in different localities. Figure 4 shows the results for females.

9. WHICH IS THE BEST SCALE?

Each researcher must select a maturity scale according to the balance between his information needs and his real working possibilities. A simplistic assumption is that the best scale is that with more stages, because it gives more detailed information. As a first approximation, this may be true, but there are some other aspects which must be taken into account:

(1) Objective of the research programme: The scale must provide biological background to the objectives of the research; i.e., if the goal is the study of gametogenesis, the scale used must bring out gonad characteristics and give less importance to other reproductive structures.

The scale must have several stages only for the part of the maturity process at which the research is aimed; i.e., if the objective is to determine spawning time, it is unnecessary to apply scales with several immature-maturing stages, and it would be more practical to use the "filling degrees" of Tinbergen and Verwey. On the other hand, if the goal is to compare the effect of the environment on the beginning of maturation, the early stages of the scale have to be more detailed.

(2) Structure of the samples: The scale can be detailed only for that period of the maturity process which is well represented in the samples; i.e., if juvenile or maturing animals predominate in the samples, a scale with several late stages is recommended only if there will be a significant number of squids in each late stage. A preliminary study will indicate which stages predominate in the samples.

(3) Condition of material: The scale must include parameters which can be used given the condition of the material. When the scale comprises parameters, such as the relative length of an organ, the possible effect of fixation on that organ must be considered and its effect on the reference structure. Lipinski (1979) notes that "it was found that the maturity scales presented here (Tables 9 and 18) apply mainly to fresh squid. The differences between stages 2 and 4 of the squid preserved for a long time in formalin, and stages 5-6 of all squid (except fresh) in particular, were hardly noticeable."

(4) Working facilities: Scales selected must be in accordance with working facilities; i.e., depending on whether they are going to be used on board a commercial fishing boat or in a comfortable land biological laboratory. More detailed scales usually require better equipment and laboratory facilities. Further, more time is needed to use them, which is particularly important when working with big samples.

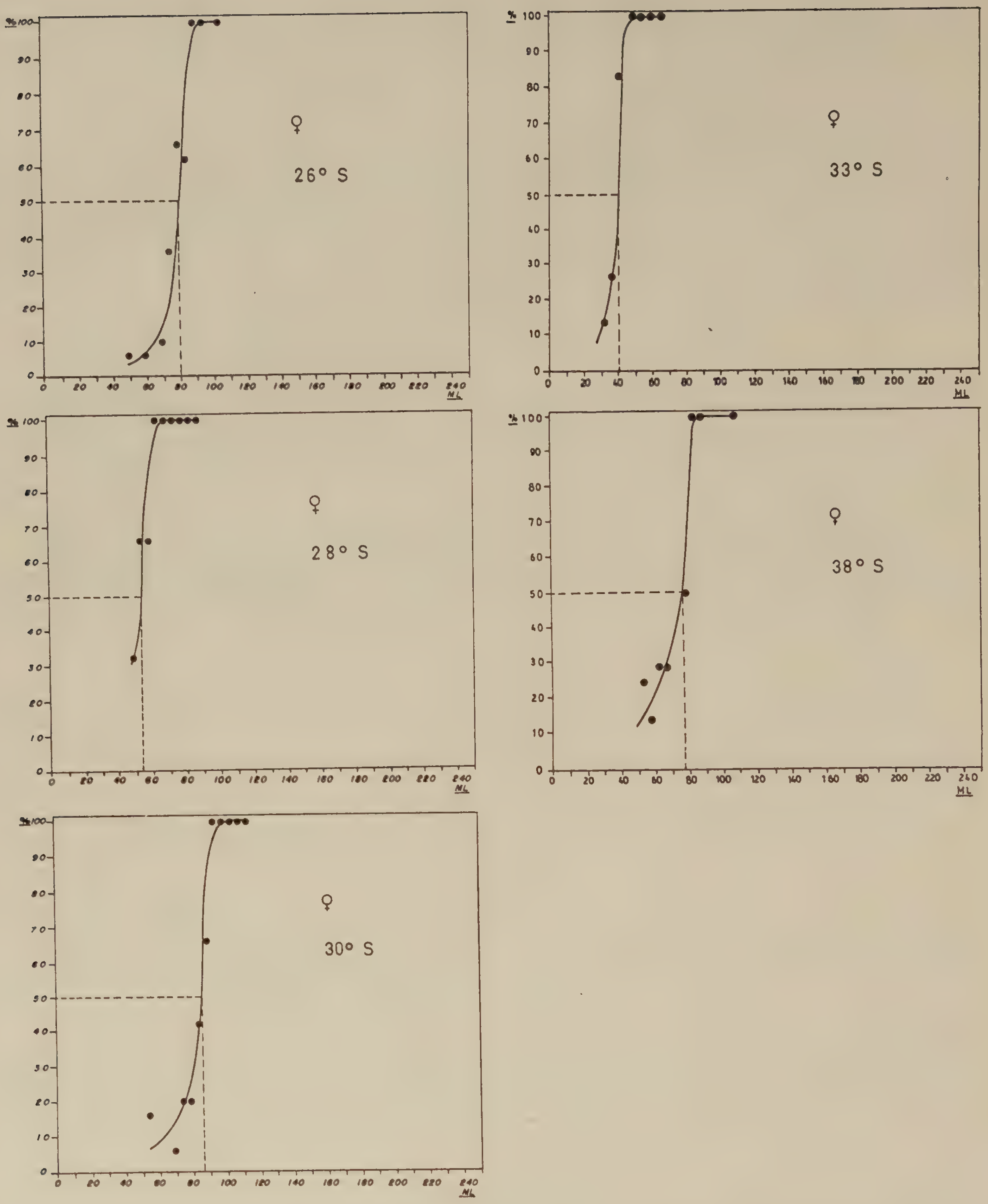


Figure 4 Percentage of each size interval (ML) of female of *Loligo brasiliensis* that started maturation (maturing stage). Latitudes indicate the approximate sampling area on the South American Atlantic coast.

10. REFERENCES

Amaratunga, T., M. Roberge and L. Wood, An outline of the fishery and biology of the
1978 short-finned squid *Illex illecebrosus* in eastern Canada. Tech.Rep.Fish.Mar.Serv.Can., (833)Pt 2:17 p.

Araya, H., Migration and fishing ground of winter subpopulation of the squid *Todarodes*
1976 *pacificus*, in the northern waters of Japan. Bull.Hokkaido Reg.Fish.Res.Lab., 41:119-29

Araya, H. and M. Ishii, Information on the fishery and ecology of the squid *Doryteuthis*
1974 *bleekeri* in the waters of Hokkaido. Bull.Hokkaido Reg.Fish.Res.Lab., 40:1-13

Arnold, G.P., Squid: a review of their biology and fisheries. Lab.Leafl.Dir.Fish.Res.
1979 C.B.(New Ser.), (48):37 p.

Arnold, J.M., Mating behaviour and social structure in *Loligo pealei*. Biol.Bull.Mar.
1962 Biol.Lab.,Woods Hole, 123(1):53-7

——————, Observations on the mating behaviour of the squid *Sepioteuthis sepioidea*.
1965 Bull.Mar.Sci., 15(1):216-22

Arnold, J.M. and L.D. Williams, Cephalopoda: Decapoda. In Reproduction of marine
1977 invertebrates, edited by A.C. Giese and J.S. Pearce. New York, Academic Press, vol. 4:243-90

Arnold,J.M.,*et al.*, A laboratory guide to the squid, *Loligo pealei*. Woods Hole, Marine
1974 Biological Laboratories, 74 p.

Austin, C.R., C. Lutwak and T. Mann, Spermatophores and spermatozoa of the squid *Loligo*
1964 *pealei*. Proc.R.Soc.Lond.(B.Biol.Sci.), 161:143-52

Barragán, J., Estudio de la maduración sexual del calamar del Pacifico Colombiano,
1969 *Lolliguncula panamensis*, Berry. Divulg.pesq.,Bogotá, 10(2-3):15 p

Berry, S.S., A note on the occurrence and habits of a luminous squid (*Abralia veranyi*)
1926 at Madeira. Biol.Bull.Mar.Biol.Lab.,Woods Hole, 51:257-68

Bloodgood, R.A., The squid accessory nidamental gland: ultrastructure and association
1977 with bacteria. Tissue Cell, 9(2):197-208, U.K.

Bottke, W., The fine structure of the ovarian follicle of *Alloteuthis subulata* Lam.
1974 Cell Tissue Res., 150:463-79

Brankoniecki, T.F., *Lolliguncula tydeus*, a new species of squid (Cephalopoda; Myopsida)
1980 from the Pacific coast of Central America. Bull.Mar.Sci., 30(2):242-30

Buchner, P., Symbiosis in luminous animals. Endosymbiosis of animals with plant micro-
1965 organisms. New York, Wiley Interscience Publishers, Chap. 9:543-71

Burukovski, R.N. and A.N. Vovk, (Some questions on the oogenesis of the Atlantic longfin
1974 squid (*Loligo pealei*) of Georges Bank): Arkh.Anat.Gistol.Embriol., 66(5):44-50 (in Russian). Issued also as Transl.Ser.Fish.Mar.Serv.Can.(3711)

Burukovski, R.N., *et al.*, (Methodological principles of developing a maturity scale for the
1977 reproductive system of squid females with *Sthenoteuthis pteropus* taken as an example). Zoll.Zh., 56:1781-91 (in Russian). Issued also as Transl.Serv.Fish.Mar.Serv.Can., (4578)

Castellanos, Z.J., Contribución al estudio biológico de *Loligo brasiliensis* Bl. Bol.Inst.
1967 Biol.Mar.Argent., (14):35 p.

Clarke, M.R., The identification of cephalopod "beaks" and the relationships between
1962 beak size and total body weight. Bull.Br.Mus.(Nat.Hist.)(Zool.), 8(10):421-97

____________, A review of the systematics and ecology of oceanic squids. Adv.Mar.Biol.,
1966 4:91-300

Clarke, M.R., N. MacLeod and O. Paliza, Cephalopod remains from the stomachs of sperm
1976 whales caught off Peru and Chile. J.Zoll.Lond., 180:477-93

Cohen, A.C., The systematics and distribution of *Loligo* (Cephalopoda, Myopsida) in the
1976 western north Atlantic, with descriptions of two new species. Malacologia, 15(2):299-367

Cowden, R.R., Cytological and cytochemical studies of oocyte development and development
1968 of the folliculat epithelium in the squid, *Loligo brevis*. Acta Embriol.Morphol. Exp., 10:160-73

Dillon, L.S. and R.O. Dial, Notes on the morphology of the Common Gulf Squid *Lolliguncula*
1962 *brevis*. Texas J.Sci, 14:156-66

Dragovich, A. and J.A. Kelly Jr., A biological study and some economical aspects of squid
1963 in Tampa Bay, Florida. Proc.Gulf Carib.Fish.Inst., 15:87-103

Drew, G.A., Sexual activities of the squid, *Loligo pealei* (Les.) 1. Copulation, egg-
1911 laying and fertilization. J.Morphol., 22:327-59

____________, Sexual activities of the squid, *Loligo pealei* (Les.) 2. The spermatophore,
1919 its structure, ejaculation and formation. J.Morphol., 32:379-435

Durward, R.D., T. Amaratunga and R.K. O'Dor, Maturation index and fecundity for the female
1978 squid *Illex illecebrosus*. Tech.Rep.Fish.Mar.Serv.Can., (833):1-10

Durward R.D., *et al.*, Reproduction in the squid, *Illex illecebrosus*: first observation in
1979 captivity and implications for the life cycle. Sel.Pap.ICNAF, 6:7-13

Fields, W.G., A preliminary report on the fishery and on the biology of the squid, *Loligo*
1950 *opalescens*. Calif.Fish Game, 36(4):366-77

____________. The structure, development, food relations, reproduction and life history
1965 of the squid *Loligo opalescens*. Fish Full.Calif.Dep.Fish Game, (131):107 p.

Franzen, A., Comparative morphological investigations into spermiogenesis among Molluscs.
1955 Zool.Bidr.Uppsala, 30:399-456

Frey, H.W. and C.W. Recksiek, Summary of market squid research program. Fish Bull.Calif.
1978 Dep.Fish Game, 169:171-2

Grieb, T.M., A study of spermatogenesis in the spawning population of the squid, *Loligo*
1976 *opalescens*. Master Thesis, San Francisco State University, 120 p.

Grieb, T.M. and R.D. Beeman, A study of spermatogenesis in the spawning population of
1978 the squid, *Loligo opalescens*. Fish Bull.Fish Game, 169:11-21

Haefner, P.A., Morphometry of the common Atlantic squid, *Loligo pealei* and the brief
1964 squid, *Lolliguncula brevis* in Delaware Bay. Chesapeake Sci., 5(3):138-44

Hamabe, M., 1963 (Exhaustion process of the genital organs of common squid, *Ommastrephes sloani pacificus*.) Bull.Japan Sea Reg.Fish.Res.Lab., 11:1-11 (in Japanese): Issued also as Transl.Ser.Fish.Mar.Serv.Can., (823)

————————, 1964 (Study on the migration of the squid, *Ommastrephes sloani pacificus* as related to the phases of the moon). Bull.Jap.Soc.Sci.Fish., 30(3):209-15 (in Japanese). Issued also as Trans.Ser.Fish.Mar.Serv.Can., (817)

Hamabe, M., T. Sato and T. Kawakami, 1974 (A preliminary note on the ecology of copulation of the Ommastrephis squid *Illex illecebrosus illecebrosus* Lesueur in the Northwest Atlantic). Bull.Tokai.Reg.Fish.Res.Lab., 78:97-105 (in Japanese). Issued also as Transl.Ser.Fish.Mar.Serv.Can., (3320)

Hamabe, M. and T. Shimizu, 1959 (Littoral aggregation of the squid near the Oki Islands). Annu.Rep.Jap.Reg.Fish.Res.Lab., 5:19-27 (in Japanese). Issued also as Transl.Ser.Mar.Fish.Servs.Can., (820)

Hamabe, M. and T. Shimizu, 1966 (Ecological studies on the common squid, *Todarodes pacificus* Steenstrup, mainly in the southwestern waters of the Sea of Japan). Bull. Jap.Sea Reg.Fish.Res.Lab., 16:13-55 (in Japanese). Issued also as Transl. Ser.Mar.Fish.Serv.Can., (812)

Hayashi, Y., 1970 (Studies on the maturity condition of the common squid. 1. A method of expressing maturity condition by numerical values). Bull.Jap.Soc.Sci.Fish., 36(10):995-9 (in Japanese)

————————, 1971 (Studies on the maturity condition of the common squid. 3. Ponderal index and weight indices of internal organs during maturation and exhaustion). Bull.Jap.Soc.Sci.Fish., 37(10):960-3

Holme, N.A., 1974 The biology of *Loligo forbesi* Steenstrup in the Plymouth area. J.Mar. Biol.Ass.U.K., 54:481-503

Ikehara, K., *et al.*, 1977 (Ecology and maturity process in *Loligo edulis budo* fished in the waters around the Oki Islets in the Western Japan Sea). Bull.Jap.Sea Reg. Fish.Res.Lab., 28:29-49

Juanicõ, M., 1979 Contribuçao ao estudo da biologia dos Cephalopoda Loliginidae do Atlantico sul ocidental, entre Rio de Janeiro e Mar del Plata, D.Sc.Thesis, Instituto Oceanogrãfico de São Paulo, 102 p.

————————, 1980 Evaluaciõn de recursos de calamar: la estructura multi-poblacional. Res.J.Cienc.Nat.Uruguay, 1:93-4

Kashiwada, J. and C.W. Recksiek, 1978 Possible morphological indicators of population structure in the market squid, *Loligo opalescens*. Fish Bull.Calif.Dep.Fish Game, 169:99-111

Katoh. G., 1959 (A few comments on the biological grouping of the common squid derived from its ecological aspect. 1. Annu.Rep.Jap.Sea Reg.Fish.Res.Lab., 5:1-17 (in Japanese). Issued also as Transl.Ser.Fish.Mar.Serv.Can., (1841)

Kjennerud, J., 1958 Description of a giant squid, *Architeuthis*, stranded on the west coast of Norway. Univ.Bergen Arb.(Naturutensk.Rekke), 9:1-14

Klyuchnic, T.S. and V.A. Zasypkina, 1972 (Some data on Argentine squid *Illex argentinus* Castellanos, 1960). Tr.Atl.Nauchno Issled.Inst.Rjbn.Khoz.Okeanogr., 42:190-2 (in Russian). Issued also as Transl.Ser.Fish.Mar.Serv.Can., (3299)

Knipe, J.H. and R.D. Beeman, 1978 Histological observations on the oogenesis in *Loligo opalescens*. Fish Bull.Calif.Dep.Fish Game, 169:23-33

LaRoe, E., A contribution to the biology of the Loliginidae of the tropical Western
1967 Atlantic. Master Thesis, University of Miami, 220 p.

Lipinski, M., Universal maturity scale for the commercially important squids. The results
1979 of maturity classification of the *Illex illecebrosus* population for the years 1973-77. ICNAP Res. Doc. 79/2/38, Serial 5364:40 p.

Mangold, K., Biologie des Céphalopodes benthiques et nectoniques de la Mer Catalane.
1963 Vie Milieu, Suppl. 13:295 p.

Mangold K. and D. Froesch, A reconsideration of factors associated with sexual matura-
1977 tion. Symp.Zool.Soc.Lond., 38:541-55

Mangold, K. *et al.*, Factors affecting sexual maturation in Cephalopods. Pubbl.Stn.
1975 Zool.Napoli, Suppl. 39:259-66

McGowan, J.A., Observations on the sexual behavior and spawning of the squid, *Loligo*
1954 *opalescens*, at La Jolla, California. Calif.Fish Game, 40(1):47-54

Mercer, M.C., Sexual maturity and sex ratio of the ommastrephis squid, *Illex illecebrosus*,
1973 at Newfoundland (Subarea 3). ICNAF Res. Doc. 73/71, Serial No. 3023:14 p.

__________, Size and maturity of the ommastrephid squid, *Illex illecebrosus*, at
1975 Newfoundland. ICES C.M. 1975/K:50:28 p.

Mensil, B., Growth and life cycle of squid, *Loligo pealei* and *Illex illecebrosus* from
1977 the Northwest Atlantic. Sel.Pap.ICNAF, 2:55-69

Nesis, K.N., The biology of the giant squid of Peru and Chile, *Dosidicus gigas*.
1970 Oceanology, Wash., 10:108-18

__________, Occurrence of a rare squid, *Chaunoteuthis mollis* Appellof in the Indian
1970a Ocean. Veliger, 12(3):290-2

Oordt. G.J. van, The spermatheca of *Loligo vulgaris*. 1. Structure of the spermatheca
1938 and function of its unicellular glands. Q.J.Microsc.Sci., 80:593-9

Rao, K.V., Biology and fishery of the Palk-Bay squid, *Sepioteuthis arctipinnis* Gould.
1954 Indian J.Fish., 1(1-2):237-66

Roper, C.F.E., A note on eggs deposition by *Doryteuthis plei* and its comparison with
1965 other North American loliginids squids. Bull.Mar.Sci., 15(3):589-98

Roper, C.F.E., C.C. Lu and K. Mangold, A new species of *Illex* from the Western Atlantic
1969 and distribution aspects of other *Illex* species. Proc.Biol.Soc.Wash., 82:295-322

Rowe, V.L. and K. Mangold, The effect of starvation on sexual maturation in *Illex*
1975 *illecebrosus* (Lesueur). J.Exp.Mar.Biol.Ecol., 17:157-63

Schuldt, M., Un problema operativo en evaluaciones estereométricas con cómputos no
1977 automatizados. Physis (A), 37(93):51-7

__________, Contribución al conocimiento del ciclo reproductor de *Illex argentinus*.
1979 Monogr.Commun.Invest.Cient.,Argent., 10:110 p.

Selman, K. and J.M. Arnold, An ultrastructural and cytochemical analysis of oogenesis
1977 in the squid, *Loligo pealei*. J.Morphol., 152:381-400

Squires, H.J., Growth and hypothetical age of the Newfoundland bait squid *Illex*
1967 *illecebrosus illecebrosus*. J.Fish.Res.Board Can., 24(6):1209-17

Steenstrup, J., (The interrelationships of the Ommastrephes-like Cephalopods. An
1880 orientation). Overs.K.Dan.Vidensk.Selsk.Forh. 1880-81:73-110 (Transl.In The cephalopod papers of J. Steenstrup. Copenhagen Danish Science Press, 1962)

Summers, W.C., The growth and size distribution of current year class *Loligo pealei*.
1968 Biol.Bull.Mar.Biol.Lab.,Woods Hole, 135:366-77

Takahashi, N. and T. Yahata, (Histological studies on the maturation of the ovary in
1973 the squid *Todarodes pacificus*). Bull.Fac.Fish.Hokkaido Univ., 24(2):63-8 (in Japanese). Issued also as Transl.Ser.Mar.Fish.Serv.Can., (3089)

Tinbergen, L. and J. Verwey, Zur Biologie von *Loligo vulgaris* Lam. Arch.Neerlan.Zool.
1945 7:213-286. Partially transl.in: Transl.Ser.Fish.Mar.Serv.Can., (2733)

Torchio, M., Eccezionale reperto di *Chaunoteuthis mollis* (Appeloff) nello Stretto di
1967 Messina. Natura, Milano, 58(3):193-207

__________, Considerazione biologiche su alcuni cephalopodi olopelagici. Conchiglie,
1976 12(11-12):251-62

Voss, G.L., A review of the cephalopods of the Gulf of Mexico. Bull.Mar.Sci.Gulf Carib.,
1956 6(2):85-178

__________, A monograph of the Cephalopods of the North Atlantic. 1. The family
1962 Lycoteuthidae. Bull.Mar.Sci.Gulf Carib., 12(2):264-305

Vovk, A.N., (Method of determining maturing stages in gonads of the squid *Loligo pealei*).
1972 Zool.Zh., 51(1):127-32 (in Russian). Issued also as Transl.Ser.Fish.Mar.Serv. Can., (2337)

__________, (Fecundity of the North American squid *Loligo pealei*). Tr.Atl.Nauchno-
1972a Issled.Inst.Rybn.Khoz.Okeanogr., 42:133-40 (in Russian). Issued also as Transl.Ser.Fish.Mar.Serv.Can., (3302)

Waller, R.A. and R.I. Wicklund, Observations from a research submersible - mating and
1968 spawning of the squid, *Doryteuthis plei*. Bio.Science, 18(1):110-1

Whitaker, J.D., A contribution to the biology of *Loligo pealei* and *Loligo plei* off the
1978 southeastern coast of the United States. Master Thesis, College of Charleston, U.S.A., 164 p.

Williams, L.W., The anatomy of the common squid, *Loligo pealei* Lesueur. Leiden,
1909 Brill., 92 p.

Yasui, T., Fluctuaciones de la abundancia de la subpoblación de invierno de *Todarodes*
1975 *pacificus*. FAO Inf.Pesca, (170) Suppl. 1:24-9

Young, R.E., *Leachia pacifica* (cephalopoda, Teuthoidea): spawning habitat and function
1975 of the brachial photophores. Pacif.Sci., 29(1):19-25

Zuyev, G.V. and M.M. Shevchenko, The biology and distribution of the sea squid
1973 *Ommastrephes pteropus* (Steenstrup, 1855) in the waters of the tropical Atlantic. Hydrobiol.J.,Wash., 9(6):10-4

Table 1

Phases of oogenesis of *Loligo opalescens*
(from Knipe and Beeman, 1978)

Ia	Probable primordial germ cells or primary oogonia are approximately 9 μm in length and appear to have no cleary defined cytoplasmic area
Ib	Secondary oogonia (approx. 16 μm in length) have a well defined nucleus with one or more nucleoli. The nucleus is surrounded by a thin layer of cytoplasm.
Ic	Secondary oogonia are now larger (approx. 59 μm in length) and show an increased ratio of cytoplasmic to nuclear volume. Numerous nucleoli 1-5 μm in diameter are present.
II	The oocytes contain a large germinal vesicle which is surrounded by an irregular corona. Follicle cells have attached to the oocyte, and have begun to proliferate on its surface.
III	The follicle cells have completely surrounded the oocyte and are changing from squamous to cuboidal-shaped cells.
IV	Follicle cells continue to proliferate and begin to penetrate the oocyte. Their morphology changes from cuboidal to columnar. Marking the end of their maximum penetration into the oocyte is the formation of a syncytium.
V	The syncytium formed by follicle cells is active in vitellogenesis and the formation of a chorion. The elaborated yolk forces the follicular syncytium to the periphery of the oocyte. The end of vitellogenesis coincides with the end of this phase. The follicle cell-oocyte complex appears laminar with the degenerating follicular syncytium located externally. The chorion, oocyte cytoplasm, and yolk are present sequentially within.
VI	Final degeneration of the follicular syncytium takes place and the mature oocyte is ovulated.

Table 2

Approximate equivalence among different oogenesis scales for squid
(The bar length do not represent delay or importance of the phases)

	Knipe and Beeman (1978) *Loligo opalescens*	Selman and Arnold (1977) *Loligo pealei*	Takahashi and Yahata (1973) *Todarodes pacificus*	Bottke (1974) *Alloteuthis subulata*	Burukovski and Vovk (1974) *Loligo pealei*	Burukovski *et al.* (1977) *Sthenoteuthis pteropus*	Schuldt (1977, 1979) *Illex argentinus*
Oogonias	Ia		I				I
	Ib						II
	Ic						
Oócytes	II	I	II	I	I II	Premeiotic Previtellogenesis 1	Mononucleolar oocytes
	III	II	III	II	III	Previtellogenesis 2 Primordial follicle	Polynucleoar oocytes
			IV				
						Previtellogenesis 3 Simple follicle	Lisis of nucleoli
							Unnucleolar ooc. without follicle folds
	IV	III					
					IV	Compound follicle	
							Unnucleolar ooc. with follicle folds
	V	IV	V	III	V	Hydratation	
						Vacuolation	Incipient vitellogenesis
			VI			Accumulation of yolk	
	VI	V					
					VI	Expulsion of the follicle	Advanced vitellogenesis
						Mature oocyte	

Table 3

Stages of ovary development for *Sthenoteuthis pteropus* (from Burukovski *et al.,* 1977)

Juvenile	The most advanced oocytes are found in the first phase of protoplasmic growth. Accumulations of premeiotic oocytes around the vessels are clearly seen in cross sections. The aciniform structure of the gonad is poorly defined. The ovary is a transparent band which is practically undistinguishable from the surrounding tissues.
Immature	The most advanced oocytes are found in the phase of the simple follicle, and this stage encompasses all the processes of its formation. The gonad has a well-defined aciniform structure. Externally, the ovary is a cloudy-grey or greyish-cream band slightly expanded anteriorly. At the end of this stage, the gonad occupies the posterior third of the mantle cavity and becomes a noticeable granular structure.
Preparatory	The most advanced oocytes are found in the compound follicle and hydration phases. This stage is very brief and has never been encountered in its "pure" form.
Mature	The most advanced oocytes are found in the phase of the mature oocyte, but there are still no residual bodies in the gonad. The ovary occupies approximately one-half of the length of the mantle cavity and is cream coloured. The mature oocytes are seen as dark disseminations under the membrane of the gonad.
Mature	Residual bodies appear in the gonad. Its colour remains the same. The number of mature oocytes increases, forming a mosaic pattern under the gonadal membrane.
Extrusion	This stage is still hypothetical, as we have never examined a post-spawning squid.

Table 4

Female maturity scales which recognize only two stages
Definitions of mature

Fields (1950,1965) *Loligo opalescens* Haefner (1964) *Loligo pealei* *Lolliguncula brevis* Klyuchnik and Zasypkina (1972) *Illex argentinus* Araya and Ishii (1974) *Doryteuthis bleekeri*	Mature eggs in the oviduct
Dragovich and Kelly (1962) *Lolliguncula brevis*	Ova approximately 2 mm in diameter were found in the oviduct. When ova approached this size, they were translucent and yellowish-orange in colour
Summers (1968) *Loligo pealei*	Ovary expanded and loose eggs were found in the oviduct.
Zuyev and Shevchenko (1973) *Ommastrephes pteropus*	NG length more than 1/3 of the length of the mantle. The ovary contains, against a background of very homogeneous ovarian structure of small immature eggs, very distinct mature eggs, which are large (0.75-0.80 mm), transparent, and light pink in colour. As new batches of eggs ripen, the ovary increases greatly in size. The total weight of the gonads, including the NG and the ovary, in many cases reached 12-13 percent of the body weight of mature females. But our collections lacked pre-spawning and currently-spawning females, and only sometimes did the ovaries contain 30-35 percent mature eggs. Undoubtedly the total weight of the gonads of females during the spawning period is significantly greater than was the case in the specimens which we captured.
Cohen (1976) 4 Loliginidae	Ovaries were filled with eggs, since this method is inadequate in recently spent animals; the lengths of ANG were recorded.

Table 5

Female maturity scale for Cephalopoda (squid, cuttlefish and octopus)
(Egg measures refer to the most advanced ones)
(Mangold, 1963)

0 Juvenile	The sex cannot be distinguished externally
I Immature	The sex can be distinguished externally. Ovary always very small
II Very small eggs	Eggs less than 1/4 of its maximum length
III Small eggs	Eggs from 1/4 to 1/2 of its maximum length
IV Medium eggs	Eggs from 1/2 to 3/4 of their maximum length
V Big eggs	Eggs greater than 3/4 of their maximum length
VI Mature eggs	Eggs ready to be spawned; the "recticular system" on their surface disappeared

Table 6

Female maturity scale for *Loligo pealei* and *Dorytheuthis pleiy*
(Whitaker, 1978)

I	Unsexed *D. pleiy*, all specimens less than 40 mm ML *L. pealei*, all specimens less than 100 mm ML
II	No sexual development; no ova apparent; gonad very small; ANG showing no colour.
III	Gonad easily observed but small; gonad estimated as 1/2 or less of maximum size; some colour in ANG; NG small or Gonad very small (as in stage II) but ANG brightly coloured
IV	Gonad appears greater than 1/3 but less than 2/3 of maximum size; ANG with colour tan to red.
V	Gonad appears greater than 2/3 of maximum size; spermatophores often found on female's buccal membrane or spermatophore pad; spermatozoa in spermatheca; ANG dark to bright red; gonad and NG large and turgid; ovary often greenish-yellow.

Table 7

Female maturity scale for *Doryteuthis plei*, *Loligo brasiliensis* and *Lollinguncula brevis*
(Juanico, 1979)
(Spent stage ommitted here and included in Table 22)

0 Juvenile	Unsexed. Neither the ovary nor the NG started to develop
I Immature	The NG can be observed (with a stereo-microscope at the beginning of this stage). The ovary, small and filamentose, still does not have a granulate structure.
II Maturing	NG small to large. At the beginning, this stage can be distinguished from Stage I by the bulky ovary with granulate structure. By the end of the stage, it can be distinguished from Stage III by the whitish opaque colour of the ovary, and the "recticular system" on the surface of the oocytes.
III Mature	Ovary and oviduct plenty of eggs, filling completely the posterior half of mantle cavity. NG turgid and rigid. All or some oocytes are amber-coloured, semi-transparent, without "recticular system"; these mature oocytes are generally found only in the oviduct, but in some females they are found in the ovary too.

Table 8

Female maturity scale for *Todarodes pacificus*
(Hamabe and Shimizu, 1966)
(Spent stage ommitted here and included in Table 22)

I Immature	With no mature eggs. Incubatory organs less than 2% of body weight
II Mature	A few mature eggs in the oviduct, which are 2-9% of body weight. They require some time before spawning.
III Fully mature	All the internal incubatory organs (the ovary and left and right oviducts) are full of mature eggs, the weight of which are 10% or more of the body weight.

Table 9

Female maturity scale for 17 species of squid
Lipinski's "Universal Scale"
(Lipinski, 1979)
(Spent stage omitted here and included in Table 22)

I Juvenile	The sexual organs are very hard to find with the naked eye. The oviducts and NG appear (if at all) as very fine transparent strips. The ovary is translucent, membranous.
II Immature	The sexual organs translucent or whitish. The oviducts and nidamental glands form cleary visible translucent or whitish strips. The oviduct meander visible. NG small; all viscera behind them can be easily observed. The ovary clearly visible, in most cases without structures observable with the naked eye.
III Preparatory	The sexual organs are not translucent. Meander of the oviduct is extended. The NG enlarged, covering some internal organs. The structures inside the ovary (immature ova) clearly visible.
IV Maturing or mature	The NG large, also covers kidneys and distal part of the liver; the external glandular oviducts are fleshy and swollen. Plenty of eggs in the oviducts; the meanders hardly noticeable. The eggs not transparent (roughly 95%) and are pressed together at least in the proximal part of the oviduct. There may or may not be many different stages of eggs in the distal part of the oviduct.
V Mature or fully-mature	As above, but the eggs are translucent (more than 60%) at least in the proximal part of the oviduct. Cut open, the NG secretes a viscous substance.

Table 10

Female maturity scale for *Todarodes pacificus*
(Hayashi, 1970)
(Spent stage omitted here and included in Table 22)

Stage	oW versus odW	maturity condition
Immature	oW > odW	$0<M<0.5$
Mature	oW = odW	$M = 0.5$

oW = ovary weight
odW = oviducts weight
maturity condition (M) = odW/(oW + odW)

Table 11

Female maturity scale for *Sthenoteuthis pteropus*
(Burukovsky *et al.*, 1977)

Spent stage omitted here and included in Table 22
Body weight is measured without the food bolus
Gonad coefficient = (gonad weight/body weight) 100
Maturity coefficient = (reproductive system weight/body weight) 100

Stage of maturity	Nidamental glands	Ovary, phase of oocyte development, macroscopy, size of oocytes (fixed in Formalin)	Gonad coefficient	Oviducts (0) and oviducal glands (OG)	Maturity coefficient %
0		Juvenile individuals	Sex visually undistinguishable		0.02-0.04
I	Transparent, filamentous, barely noticeable against background of stomach, length equal to 3.6-11.2 % of mantle length (average 7.8%)	Cloudy-grey cordlike band, slightly expanding anteriorly. Most advanced oocytes in second phase of protoplasmic growth. Transparent, oval or pyriform. Nucleus clearly seen, occupies greater part of cell. Diameter of oocytes 0.1-0.27 mm	0.01-0.5 average 0.23	Visually undistinguishable	0.03-0.65 average 0.3
II	Greyish-white, convex, resilient, cordlike. Longitudinal band clearly visible. Length 5.5-19.7%, average 10.3%	Cloudy-grey colour; greatly increases in size. Anterior lobes clearly seen. Weakly granular structure discernable. Most advanced oocytes in first half of simple follicle phase. Oocytes oval or polygonal. Nucleus in widest part of cell, well defined. Diameter of oocytes 0.25-0.38 mm	0.17-1.05 average 0.47	0: flat transparent film; OG: translucent	0.2-1.2 average 0.5
III	Whitish-grey or white, fusiform, resilient. Length 9.2-31.3, average 16.8%	Greyish or greyish-cream; occupies posterior third of mantle cavity. Granular structure clearly visible. Most advanced oocytes in simple follicle phase, transparent, ellipsoidal. Diameter of oocytes 0.30-0.42 mm	0.32-2.65 average 0.86	0: easily distinguishable translucent flat bands; OG: thickened grey or whitish-grey	0.4-3.5 average 1.1
IV	Milky-white, resilient, leaf-shaped. In this and the following stage we observe a slight increase in size with a noticeable increase in volume and weight. Secretion does not exude when glands are cut. Length 18.0-35.5%, average 25.0%	Cream-coloured. Occupy approximately 1/2 length of mantle cavity. Most advanced oocytes in phase of compound follicle or explusion of follicular folds. Reticulate pattern well-defined. Individual oocytes pass to phase of mature	0.84-8.0 average 2.8	0: well-defined, transverse septa visible; OG: white, resilient	1.2-9.7 average 4.3

Table 11 (continued)

Stage of maturity	Nidamental glands	Ovary, phase of oocyte development, macroscopy, size of oocytes (fixed in Formalin)	Gonad coefficient	Oviducts (O) and oviducal glands (OG)	Maturity coefficient %
V_1	External appearance as before. Secretion does not exude when cut. Length 22.2-45.8% average 33.6%	Colour as before, only slightly darker, number of mature eggs increases noticeably, forming mosaic pattern on surface. Diameter of mature oocytes falling into gonadal cavity 0.78-0.90 mm	1.68-7.6 average 4.0	O: small number of mature eggs appear, up to 5-8% of all the oocytes OG: convex, resilient, white	2.8-10.2 average 6.8
V_2	Sticky substance exudes from glands when they are cut. Length 25.0-46.5% average 37.8%	The number of mature eggs continues to increase. Mosaic pattern is preserved.	1.7-16.2 average 4.8	O: large, resilient, filled with mature eggs (10-60% of all the oocytes by volume)	3.6-15.8 average 10.1
V_3	Length 38.5-48.5 % average 42.7%	Volume of gonad decreases considerably. Mosaic pattern less defined due to discharge of mature eggs into oviducts	1.9-5.6 average 4.3	Accumulation of mature eggs is completed (up to 60-80% of the overall volume of oocytes)	15.4-29.8 average 20.0

Table 12

Female maturity scale for *Illex illecebrosus*
(R.D. Durward, T. Amaratunga and R.K. O'Dor, 1978)

Oogenesis phases from Selman and Arnold, 1977 (see Tables 1 and 2)
Measurements of follicles on fixed material
O = ovary + oviduct
B = body

Maturation stage (M)	NGL/ML range	NG(mm) range	OW/BW range	OW(g) range	Most advanced oocytes		Distinguishing morphological feature
					Phase	Follicle size (mm) (µm)	
I	$M \leq 0.09$	11-25	$M \leq 0.00275$	0.14-0.9	1	0.20 x 0.14 2.9 µg	NG thin and transparent
II	$0.09 < M \leq 0.125$	20-35	$0.00275 < M \leq 0.005$	0.68-1.6	2	0.26 x 0.16 5.66 µg	NG transparent to translucent ovary - granular
III	$0.125 < M \leq 0.2$	25-60	$0.005 < M \leq 0.015$	1.1-5.42	3	0.35 x 0.25 16.04 µg	NG translucent to opaque
IV	$0.2 < M \leq 0.35$	55-90	$0.015 < M \leq 0.10$	6.0-30.0	4	between stages 3 and 5	NG white oviducts forming
V	$0.35 < M$	110-120	$0.10 < M$	50.0-104.0	5	0.9 x 0.625 240.0 µg	eggs in the oviducts

Table 13

Female maturity scale for *Illex argentinus* (summarized)
(Schuldt, 1979)

Nidamental index (NI) = $[\text{NG weight in g}/(\text{ML in cm})^3]10^4$
Cellular diversity index (CDI) = see Figure 3c

Maturity condition stage	Ovary cells (see Table 2)	Gonadal stage	CDI	Nidamental stage	NI %
0 Virginal immature	Quoted by the presence of oocytes with lisis of nucleoli	0 virginal immature	.1245	I	15
I Incipient mature	With unnucleolar oocytes without follicle folds	I virginal incipient mature	.2087		
		II incipient mature	.2152	II	15-20
II Half mature	With the first oocytes with incipient vitellogenesis	III half mature	.3293	III	20-30
III Advanced mature	All kinds of oocytes are found	IV advanced mature	.5156	IV	30-35
		V advanced mature	.5206	V	35

Table 14

Approximate equivalences among different female maturity scales
(The bar lengths do not represent delay or importance of the stages)

Increasing maturity ⟶

<table>
<tr><td>Phase of most advanced oocytes. Scale of Knipe and Beeman (1978) (Tables 1 and 2)</td><td>I or II</td><td colspan="4">III</td><td>IV</td><td>V</td><td colspan="4">VI</td></tr>
<tr><td colspan="12"></td></tr>
<tr><td>Tinbergen and Verwey (1945)
Oviductal filling degree</td><td>-</td><td colspan="6">none</td><td>few</td><td colspan="2">mod-erate</td><td>many</td></tr>
<tr><td>Schuldt (1979)
Maturity condition</td><td>-</td><td colspan="2">0</td><td>1</td><td colspan="3">2</td><td colspan="4">3</td></tr>
<tr><td>Durward, Amaratunga and O'Dor (1978)</td><td>-</td><td colspan="2">I</td><td>II</td><td>III</td><td colspan="2">IV</td><td colspan="4">V</td></tr>
<tr><td>Burukovski *et al.* (1977)</td><td>juvenile</td><td colspan="2">I</td><td>II</td><td>III</td><td colspan="2">IV</td><td>V_1</td><td colspan="2">V_2</td><td>V_3</td></tr>
<tr><td>Lipinski (1979)
"Universal scale"</td><td>juvenile</td><td colspan="2">immature</td><td colspan="4">preparatory</td><td colspan="2">mature</td><td colspan="2">fully mature</td></tr>
<tr><td>Nesis (1969)</td><td>-</td><td colspan="2">I</td><td colspan="4">II</td><td colspan="2">III</td><td colspan="2">IV</td></tr>
<tr><td>Hamabe and Shimizu (1966)</td><td>-</td><td colspan="6">immature</td><td colspan="2">mature</td><td colspan="2">fully mature</td></tr>
<tr><td>Mangold (1963)</td><td>juvenile</td><td>I</td><td>II</td><td colspan="2">III</td><td>IV</td><td>V</td><td colspan="4">VI</td></tr>
<tr><td>Burukovski and Vovk (1974)
Vovk (1972)</td><td>-</td><td colspan="2">I</td><td colspan="2">II</td><td colspan="2">III</td><td colspan="4">IV</td></tr>
<tr><td>Juanicó (1979)
Whitaker (1978)</td><td>juvenile</td><td colspan="2">immature</td><td colspan="4">maturing</td><td colspan="4">mature</td></tr>
<tr><td>Kashiwada and Recksiek (1978)
Barragán (1969)</td><td>-</td><td colspan="2">immature</td><td colspan="4">maturing</td><td colspan="4">mature</td></tr>
<tr><td>Dragovich and Kelly (1962)</td><td>unsexed</td><td colspan="6">immature</td><td colspan="4">mature</td></tr>
<tr><td>Fields (1950)
Haefner (1964)
Fields (1965)
Summers (1968)
Hayashi (1970)
Klyuchnuck and Zasypkina (1972)
Zuyev and Shevchenko (1973)
Araya and Ishii (1974)
Cohen (1976)</td><td>-</td><td colspan="6">immature</td><td colspan="4">mature</td></tr>
</table>

Table 15

Male maturity scales which recognize only two stages

		Immature	Mature
A	Haefner (1964) *Loligo pealei* *Lolliguncula brevis*		Presence of spermatophores in spermatophoric sac
	Fields (1965) *Loligo opalescens*	Without spermatophores	With spermatophores in spermatophoric sac
	Hamabe and Shimizu (1966) *Todarodes pacificus*	Without spermatophores	With spermatophores
	Summers (1968) *Loligo pealei*		Spermatophores present; a thickening and white coloration of the vas deterens
	Zuyev and Shevenchenko (1973) *Ommastrephes pteropus*		Spermatophoric sac contains some quantity of spermatophores filled with white sperm. They are 25-35 mm long and number from several tens to 200 or 250.
	Cohen (1976) Loliginidae		Spermatophores present in spermatophoric sac
B	Dragovich and Kelly (1962) *Lolliguncula brevis*	Spermatophores, if present, were not fully developed	Spermatophores possessed a distinctly developed head, spiral tube, cement gland and sperm sac
	Klyuchnik and Zasypkina (1972) *Illex argentinus*	Spermatophores underdeveloped	With fully formed spermatophores

Table 16

Male maturity scales with only one maturing stage
(Spent stage omitted here and included in Table 23)

	A				B
	Mangold (1963) Cephalopoda	Nesis (1970) *Dosidicus gigas* Schuldt (1979) *Illex argentinus*	Kashiwada and Recksiek (1978) *Loligo opalescens*	Juanicó (1979) Loliginidae	Araya and Ishii (1974) *Doryteuthis bleekeri*
Juvenile	Sex cannot be distinguished externally			Unsexed; neither the testis nor the SO, nor the SS, started to develop	
Immature	Sex can be distinguished externally; testis more or less bulky		Testis short and thin to long and thick; without S	Testis membranous or little bulky; SO and SS can be observed (with a stereo-microscope) very small and without S	Without S in SS; sperm duct transparent
Maturing	Secretion of S started; sperm duct filled with spermatozoa	Few S in SS	Testis long and thick; few S loosely packed	Some S in the SS, but few and small; testis easily noticeable with naked eye	Without S in SS; sperm duct white
Mature	S in SS	SS filled with ripe S	Testis long and either thick or thin; large numbers of S densely packed	SS filled with S fully developed; testis at maximum length; it seems that males continually produce S once maturity is reached	With S in SS

Table 17

Male maturity scale for *Loligo pealei* and *Doryteuthis plei*
(Whitaker, 1978)

Juvenile 0	*D. plei :* all specimens less than 40 mm *L. pealei:* all specimens less than 100 mm
I	No sexual development; no spermatophores
II	Gonad easily observed but small; gonad estimated as 1/3 or less of maximum size or Gonad very small (as in stage I) but a few S present in SS
III	Gonad appears greater than 1/3 but less than 2/3 of maximum size; several S present (more than 5) but SS not full; vas deferens is obvious
IV	Gonad appears greater than 2/3 of maximum size; vas deferens very obvious and appearing silver or porcelain white; SS closely packed with S.

Table 18

Male mautrity scale for 17 species of squid
(Lipinski, 1979)

Lipinski's "Universal scale"
Spent stage omitted here and included in Table 23

Juvenile	The sexual organs are very hard to find with the naked eye. Spermatophoric complex appears (if at all) as a transparent or translucent spot. The testis is transparent, membranous.
Immature	The sexual organs translucent or whitish; the separate parts of the spermatophoric complex are clearly visible; the testis small; its structure invisible
Preparatory	The sexual organs are not translucent; the vas deferens whitish or white, SO with white streak; the testis in most cases is white or pink; its structure is invisible
Maturing	The vas deferens white, meandering, enlarged; SS long with structureless whitish particles inside, but without formed S; the testis tight, crispy; the testis surface covered with structure
Mature	As above, except that S are present in the SS

Table 19

Male maturity scale for *Loligo pealei*
(Vovk, 1972)

1	Testis not noticeable, or as small as a white disk; SO and SS noticeable left skewed. In some cases the hectocotylus begins to be formed in the left lower arm. The weight of the genital organs is almost 0.5% of total squid weight.
2	Testis clearly visible, filling almost 1/2 of the posterior part of mantle cavity. It is whitish-grey and flaccid. SO and SS well developed; the basis of the penis visible; hectocotylus visible too; weight of reproductive system: 0.5-5% of total squid weight.
3	Testis increases twice its volume, filling the posterior part of mantle cavity; it maintains its colour and is flexible. In the SS appears the first small S; S relative length is about 5% of mantle length. Length of hectocotylized part of hectocotylus: 15% of mantle length. Weight of genital organs: up to 7% of total squid weight.
4	Testis compact, pale yellow, filling the mantle cavity from stomach to the end of the gladius. SS pyriform, filled with S. S visible through the SS wall, inclined along the SS axis and densely packed. In some cases S are noticeable in the basis of the penis. A slight pressure on SS will let the S go through the penis to mantle cavity.
5	Testis rather rigid, covers part of the stomach filling all the posterior part of the mantle cavity. The packet of S dilates, making transparent the walls of the SS. S usually noticeable in the basis and tip of penis. Due to the fast growth of squid size and weight, a decrease of the relative length of hectocotylus and S. Hectocotylus length of 11.4%, S length 4.3% and reproductive system weight of 5.8% is characteristic.

Table 20

Male maturity scale for *Todarodes pacificus*
(Hayashi, 1970)

Spent stage omitted here and included in Table 23
tW = testis weight; SSW = SS weight
Maturity condition (M) = SSW/(tW SSW)

Stage	tW versus SSW	Maturity condition
Immature	tW > SSW	$0 < M < 0.5$
Mature	tW = SSW	$M = 0.5$

Table 21

Approximate equivalence among different male maturity scales
(The bar lengths do not represent delay or importance of the stages)

<table>
<tr><td>Most advanced spermatogenic cells. From Grieb (1976), Grieb and Beeman (1978) and Schuldt (1979)</td><td></td><td>Small spermatogonia</td><td>Spermatocytes</td><td>Spermatids</td><td colspan="4">Spermatozoa</td></tr>
<tr><td></td><td></td><td colspan="7"></td></tr>
<tr><td>Tinbergen and Verwey (1945)</td><td>-</td><td colspan="2">empty</td><td>almost empty</td><td colspan="2">1/4</td><td>1/2</td><td>full</td></tr>
<tr><td>Vovk (1972)</td><td>-</td><td>1</td><td>2</td><td colspan="2">3</td><td colspan="2">4</td><td>5</td></tr>
<tr><td>Lipinski (1979)
Whitaker (1978)</td><td>juvenile</td><td>immature</td><td>maturing I</td><td colspan="2">maturing II</td><td colspan="3">mature</td></tr>
<tr><td>Mercer (1975)</td><td>-</td><td>immature</td><td>maturing I</td><td colspan="2">maturing II</td><td colspan="3">mature</td></tr>
<tr><td>Araya and Ishii (1974)</td><td>-</td><td>immature</td><td>maturing</td><td colspan="5">mature</td></tr>
<tr><td>Juanicõ (1979)
Mangold (1963)</td><td>juvenile</td><td colspan="2">immature</td><td colspan="2">maturing</td><td colspan="3">mature</td></tr>
<tr><td>Nesis (1970)
Kashiwada and Recksiek (1978)
Schuldt (1979)</td><td>-</td><td colspan="2">immature</td><td colspan="2">maturing</td><td colspan="3">mature</td></tr>
<tr><td>Dragovich and Kelly (1962)
Hayashi (1970)
Klyuchnik and Zasypkina (1972)</td><td>-</td><td colspan="4">immature</td><td colspan="3">mature</td></tr>
<tr><td>Haefner (1964)
Fields (1965)
Hamabe and Shimizu (1966)
Zuyev and Shevchenko (1973)
Cohen (1976)</td><td>-</td><td colspan="2">immature</td><td colspan="5">mature</td></tr>
</table>

Table 22

Female spent stage according to different authors

Tinbergen and Verwey (1945) *Loligo vulgaris.*	The eggs are not as tightly packed in the ovary as described before, which gives the ovary a strikingly loose, disorderly aspect. These are probably the females which have just released their eggs.
Hamabe and Shimizu (1966) *Todarodes pacificus*	Those females whose skin was stripped and in which a striking decrease in the content weight of the incubatory organs and liver was noted along with a shrunken mantle. Females in the process of dying from post-spawning exhaustion.
Barragān (1969) *Lolliguncula brevis*	Gonads small, 0.9-2.8 g; NG relatively large; oocytes small, whitish and pyriform; some specimens with no spawned mature ova which would be reabsorbed later; some females with many S
Hayashi (1970) *Todarodes pacificus*	Ovary weight $\ll$ oviductal weight (in mature animals the weights are approximately the same, and in immature ones on the contrary).
Vovk (1972) and Burukovski and Vovk (1974) *Loligo pealei* Burukovski *et al.* (1977) *Sthenoteuthis pteropus*	There is a small number of eggs in the ovary. Most often there are no mature eggs in the ovary. The ANG are of pale-rose colour. The NG and oviductal gland are softened and creembly and noticeably smaller in volume and weight. The mantle looses its previous density and elasticity and becomes flabby. The weight of the reproductive system amounts to about 1/5 of the animal's weight. The dimensions of the not numerous females of this stage investigated by us are the same as of females of the fourth stage (mature)
Kashiwada and Recksier (1978) *Loligo opalescens*	NG large, greater than 20% of dorsal mantle length. Eggs large large but few in number and opaque
Lipinski (1979) 14 squid species	There are almost no eggs in the oviduct, or only degenerating ones. The NG are small, tissue slack and desintegrated. The condition of the animal is very poor; the hypothetical stage
Juanicō (1979) Loliginidae, 3 species	Spawning or spent: large females with NG flaccid or diminished. Ovary and oviduct flaccid with no or only a few mature eggs, but with immature eggs and tissue remains.

Table 23

Male spent stage according to different authors

Hamabe and Shimizu (1966) *Todarodes pacificus*	Males possessing S but whose feature and internal organs were deemed to be in a state of debility similar to that of the spent females
Hayashi (1970) *Todarodes pacificus*	Testis weight < SS mass weight (in mature animals the weights are approximately the same, and in immature ones, on the contrary).
Grieb (1976) and Grieb and Beeman (1978) *Loligo opalescens*	Animals in which only mature or very late mature spermatids were found within the seminiferous tubules, and represents the final stage of maturation process in the spawning animals. These spent animals were undergoing a degenerative process. While the seminiferous tubules of some animals contained relatively large numbers of mature spermatids, the testicular tissue of other specimens were composed of empty or collapsed tubules which contained only a very small number of relict sperm. In this latter stage, the lumen of the tubules sometimes contained large amounts of what appeared to be sloughed cytoplasm and sperical, vacuolated bodies. In all these animals the seminiferous epithelium was found to be thin and no visible sign of epithelial growth could be detected. Furthermore, the mantles of these animals were flaccid and their general condition was best described as emaciated. Finally, the SS contained very few S. The seminiferous epithelia of *L. opalescens* shows no sign of germinal cell growth or spermatogonia. This lack of any sign of a renewed gametogenic cycle, the degenerative condition of the seminiferous epithelia and the emaciated condition of spent animals leads to the conclusion that males spawn only once and die soon afterwards.
Kashiwada and Recksiek (1978) *Loligo opalescens*	Testis long and thin (in mature animals they were thick) S few in numbers and loosely packed or degenerating
Lipinski (1979) 14 squid species	There are no S in the SS or only exploded, degenerating ones. Spermatophoric complex contains many membranous structures. The condition of the animal is very poor.

THE ROLE OF CEPHALOPODS IN THE MARINE ECOSYSTEM

by

T. Amaratunga
Invertebrates and Marine Plants Division
Fisheries Research Branch
Department of Fisheries and Oceans Canada
P.O. Box 550
Halifax, Nova Scotia B3J 2S7
Canada

ABSTRACT

There are about 650 species of cephalopods in diverse habitats of the marine ecosystem. A review of these showed that commercially important species constituted a very large biomass. These were represented by highly specialized and often intelligent organisms belonging to the groups *Nautilus*, *Sepia*, squid and octopus; the squid belonging to the families ommastrephids and loliginids were the most important. Most presently important species are found in benthic or pelagic habitats in the neritic province not extending far beyond the continental slope edges. Biology, distribution and feeding habits of major species were reviewed. Predation is principally on the crustacea, while fish predation and cannibalism is of lesser importance. Predation models are presented for important cephalopod groups. Cephalopods are preyed upon by a large number of fish, sea birds and marine mammals. An efficient energy transfer therefore mainly occurs from detritus feeders, scavengers and plankton consumers to carnivorous cephalopod predators. A large biomass of cephalopods in turn are available to the uppermost trophic levels.

A mathematical interpretation of biological parameters is considered in a biomass-production model, with particular reference to the ommastrephid *Illex illecebrosus*. Effects of predation on the ecosystem are quantified, and it is demonstrated how food consumption rates are transposed into growth. Growth rates in turn can be transposed into time-segmented changes in biomass.

RESUME

Il y a environ 650 espèces de céphalopodes dans les divers habitats de l'écosystème marin. L'examen de celles-ci a démontré que les espèces commerciales importantes ont constitué une grande partie de la biomasse. Ces espèces sont représentées par des organismes intelligents et hautement spécialisés appartenant aux groupes des *Nautilus*, des seiches, des calmars et des pieuvres; les calmars appartenant aux familles ommastrephides et loliginides sont les plus importants. On retrouve les espèces importantes dans des habitats benthiques et pélagiques dans la province néritique qui ne s'étend qu'une très courte distance au delà du talus continental. On a examiné la biologie, la distribution, et les habitudes alimentaires des principales espèces. La prédation joue principalement sur quelques types de crustacés tandis que celle sur les poissons et le cannibalisme est de moindre importance. Des modèles de prédation ont étés présentés pour les groupes de céphalopodes importants. Les céphalopods sont la proie d'un grand nombre de poissons, d'oiseaux de mer et de mammifères marins. Un transfert efficace d'énergie a été proposé pour englober les mangeurs de détritus, les nécrophages, les consommateurs de plankton et les céphalopodes carnivores prédateurs. On dispose d'une large biomasse de céphalopodes pour les niveaux trophiques plus élevés.

On a étudié une interprétation mathématique des paramètres biologiques dans un modèle de biomasse-production, avec référence particulière à l'ommastrephide *Illex illecebrosus*. Les effets de la prédation sur l'écosystème ont été quantifiés et il a été démontré que les taux de la consommation de nourriture peuvent se traduire en terme de croissance. Les taux de croissance à leur tour peuvent être transformés en changements à intervalles de temps en biomasse.

RESUMEN

En los diversos habitat del ecosistema marino viven alrededor de 650 especies de cefalópodos. Un examen de estas especies reveló que las de importancia comercial constituyen una biomasa muy amplia. Están representadas por organismos muy complejos, pertenecientes a los grupos *Nautilus*, sepia, calamar y pulpo; los calamares más importantes pertenecen a las familias de los ommatostréfidos y de los loliguidos. Las especies importantes más abundantes se encuentran en los hábitat bentónicos o pelágicos de la zona nerítica que no se extiende más allá del borde del talud continental. Se estudió la biología, la distribución y los hábitos alimentarios de las especies principales. Los crustáceos son el principal objeto de presa, mientras que la ictiofagía y el canibalismo son hábitos alimentarios de menor importancia. Se prestan modelos de depredación correspondientes a importantes grupos de cefalópodos. Los cefalópodos son presa de una gran cantidad de peces, aves marinas y mamíferos marinos. Por consiguiente, se produce una eficaz transferencia de energía principalmente a partir de quienes se alimentan de detritus, los consumidores de carroña y de plancton de los depredadores cefalópodos carnívoros, al tiempo que una gran biomasa de cefalópodos queda disponible para los niveles tróficos más altos.

En un modelo de producción de biomasa se hace una interpretación matemática de los parámetros biológicos, con especial referencia al ommatostréfido *Illex illecebrosus*. Se cuantifican las consecuencias de la depredación en el ecosistema y se demuestra de qué manera los índices de consumo de alimentos se traducen en crecimiento. Los índices de crecimiento a su vez se pueden expresar como cambios de la biomasa en fracciones de tiempo.

1. INTRODUCTION

World fish landings in 1967 totalled 50 million t (Gulland, 1971), of which cephalopods made up close to 1 million t (Okutani, 1977). World cephalopod catches have traditionally consisted mainly of those species available to the Japanese fishery; and until 1973, Japan landed more than 60 percent of the world cephalopod landings (Okutani, 1977). Since the early 1970s other countries have developed commercial interest, and globally many new cephalopod fisheries began developing. In the western Atlantic alone, three major fisheries developed for *Illex illecebrosus*, *I. argentinus* and *Loligo pealei* (Amaratunga and Budden, 1981; Juanicó, 1980; and Lange, 1980, respectively.) These fisheries have demonstrated that the squid resources can represent a very large biomass.

An excellent example which is familiar to the author is the *I. illecebrosus* fishery. Up to 1973 the annual landings accounted for less than 15 000 t. Subsequent increased landings resulted in more than 170 000 t in 1979.

For this annual species (Amaratunga, 1980), assessments using traditional models have not been satisfactory; however, seasonal areal expansion and other methods have resulted in annual biomass estimations as high as 3 x 10^6 t (Anon, 1980).

Globally, cephalopod biomass estimates have been very important, e.g.,2-100 x 10^6 t (Gulland, 1971), weight of squid eaten by sperm whales 100-320 x 10^6 t (Kawakami, 1980), and 100-300 x 10^6 t-probably as high as 500 x 10^6 (Voss, 1973). These greatly exceed the total world fish landings in 1967. What is then the function of this biomass in the marine ecosystem?

1.1 Class Cephalopoda

In the phylum Mollusca, class Cephalopoda is perhaps commercially the most important group, containing the *Nautilus*, cuttlefish, squid and octopus.

The class Cephalopoda has five distinct groups (see Table 1 of Appendix)[1/] From an evolutionary standpoint, many more cephalopods species are found in the fossils than in the presently living forms. Only about 650 species now exist as compared to more than 7 500 different fossil forms (Barnes, 1974). Many present species are seldom encountered, but they occur in all world oceans occupying both neritic and oceanic provinces extending from littoral and benthic to pelagic environments. Voss (1973) presented a review of the world cephalopod fisheries showing exploitable resources.

In contrast to other molluscs, the whole cephalopod class has adapted to a swimming existence, although here again variations exist. In their diverse habitats and forms, the more economically important species appear to be very successful animals with unusual intelligence and learning capabilities (Wells, 1978). Additionally, as a result of their high metabolic rates, they are voracious feeders. The relevant adaptations here are swimming by jet propulsion and the use of prehensile arms and tentacles to seize and hold prey, thus making cephalopods formidable predators in the marine ecosystem.

A glance at the classification list (Table 1 of Appendix) shows that it will be an overwhelming task to even consider the possible variations family by family. Let us therefore look closely at the classifications, study those that are important in the marine ecosystem, and limit ourselves to the more economically important species. This is justified because the commercially important species have become so by virtue of their sheer large numbers, and form major components of the biomass of the marine ecosystem even though commercial exploitation of cephalopods presently takes place only in about 10 percent of the ocean area, and even though a large percentage of described cephalopods exist outside this area (Voss, 1973).

All modern Cephalopoda, with the exception of *Nautilus* of the subclass Nautiloidea, belong to the subclass Coleoidea containing four distinct groups: the orders Sepioidea, Teuthoidea, Octopoda and Vampyromorpha.

The Nautiloidea contains primitive forms (Young, 1965) and five species exist today in the Indo-West Pacific region in Indonesia and the Philippines and are commercially important, especially for their pearly shells (Voss, 1973).

The Sepioidea, which have three clear-cut groups, contain the cuttlefish-like forms. The true cuttlefish of the family Sepiidae carry an internal septate shell, the cuttlebone, which keeps their bodies rigid and oval in shape with eight short arms and two elongate tentacles used primarily for prey capture (Messenger, 1977). Although capable swimmers, they are bottom dwellers and their buoyancy control restricts them to the shallower continental shelf areas (Morton and Younge, 1964). The cuttlefish, *Sepia* sp. and *Sepiella* spp., are commercially important. The other groups of Sepioidea are inconsequential to this study.

The order Teuthoidea, containing the squids, can be characterized into two forms: the "open-eyed" oegopsids, and the "covered-eyed" myopsids.

The myopsids consist of two families and a relatively small number of species. The major family, Loliginidae, is believed to have developed the covered eye as an adaptation to the sediment-rich waters of the continental shelf areas (Morton and Younge, 1964) and are thus generally found in the neritic province not extending beyond the continental shelf edge. Typical commercially important examples are *Loligo pealei, L. opalescens, L. vulgaris and L. edulis* (Voss, 1973).

[1/] For convenience to the readers and to aid the author in text discussions, a copy of Dr G.L. Voss' classification list (1977) (a new and more extensive catalogue is now in preparation). The Cephalopods of the World - An Annotated and Illustrated Catalogue of Species of Present and Potential Interest to Fisheries - C.F. Roper and M. Sweeney - FAO Species Catalogue Vol. II

The oegopsids are the oceanic squid which carry the largest and the smallest known cephalopods. The giant squid, *Architeuthis* sp., is the largest known invertebrate (Barnes, 1974). The commercially most important squid belong to the family Ommastrephidae. Among six or seven important genera, *Todarodes* sp. and *Illex* sp. make up the largest cephalopod fisheries.

The above commercially important teuthoid squid are well adapted for continued and often fast swimming. This is accomplished by jet propulsion as well as by fin movements. The soft muscular, tubular body or mantle, through expansion and contraction, can jet water through a pallial funnel when swimming. Anteriorly, decapod format of eight arms and two tentacles varies in form and capabilities, but has the primary functions of prey capture.

The Octopoda, the eight-armed cephalopods, carry the two groups Cirrata and Incirrata. Cirrata is made up of the finned octopods which are mainly deep-water, soft-bodied species and are of no commercial importance. Incirrata, on the other hand, is a diverse group which includes the Octopodidae and the bottom-dwelling, commercially important octopus forms of the genera *Octopus*, *Cistopus* and *Eledone*. The common octopus, *Octopus vulgaris*, perhaps provides a good description of the general features of these forms. *O. vulgaris* has a vestigial shell (Wells, 1978) within a globular or bag-like mantle cavity. From the dorsal head region, eight prehensile arms radiate and although most octopi are capable of swimming by water jets from the mantle through the funnel, their usual method of locomotion (particularly during predation) is described as "walking"; using their arms which have complex musculature for manouvering, and the suckers for adhesion. The Octopus is an active predator.

Finally, it is necessary to mention the Vampyromorpha, represented by one known bathypelagic form. This contains a small, lacker abberant, deep-water vampire squid, *Vampyroteuthis infernalis*, of unknown relationship and derivation (Voss, 1973), and of no commericial importance.

From our elimination process, we are now left with *Nautilus* and the orders Sepioidea, Teuthoidea and Octopoda. *Nautilus*, although considered commercially important is probably the least important among the selected forms. The very limited geographic distribution has a somewhat atypical archaic form with an external shell which restricts mobility and will not be considered further here.

Among the Sepioidea, we will confine our discussion to the true cuttlefish and similary for the octopods, we will limit discussion to bottom-dwelling forms of commercial interest. In Teuthoidea we have encountered two major groups: myopsids and oegopsids, each being of great commercial importance.

These then are the key cephalopods in the marine ecosystem of present interest to fishermen. Since all stages of their life cycles are critical, the discussion will first deal with eggs and embryonic forms, then post-embryonic forms and larvae, and finally the juveniles and adults.

2. THE LIFE CYCLE

2.1 Strategies of the Egg and Embryonic Stages

Cephalopods produce telolecithal eggs with direct development through organogenesis to hatchlings that bear a resemblance to their adult form (Lane, 1957; Fioroni, 1971). For our purposes, it is important to consider cephalopod egg characteristics and their survival strategies in relation to environmental conditions.

The cephalopod eggs may be free floating or attached to the substratum or materials such as seaweed, singly or in aggregates or masses. Boletzky (1974) noted that the decopod cephalopods, Sepioidea and Teuthoidea, embed their eggs in gelatinous cases secreted by the female nidamental gland believed to protect them throughout embryonic development.

The Sepioidea have relatively large yolky eggs. Laboratory observation on Sepioidea showed females generally spawned during the night or early morning and they attached their eggs to the wall of the tank (Boletzky, *et al.*, 1971).

Among the Teuthoidea, *Loligo opalescens* occurs from British Columbia to southern California and spawns in depths from 3 m to 30 m, mainly in winter in the southern areas and late summer in the northern areas (Fields, 1965). From laboratory observations, spawning is believed to take place chiefly at night. An estimated 180-300 eggs are enclosed in a flexible, jelly-like capsule. Similar egg strings are spawned by *Loligo pealei* and *Loligo vulgaris* in the Atlantic. *L. pealei* egg strings contain 150-200 eggs (McMahon and Summers, 1971). Fields (1965) described the eggs as encased in a transparent homogeneous matrix secreted by the oviducal gland and enclosed by a firm outer translucent layer which is apparently formed by the combined secretion of the nidamental gland and accessory nidamental glands. These finger-like capsules are attached to the substratum in muddy/sandy areas by a tapered stalk. Okiyama (1965) described eggs of the oegopsid *Todarodes pacificus* as ovoid in shape and covered with a gelatinous layer slightly adhesive in nature; and Hamabe (1962) notes that egg masses may carry 300-400 eggs distributed in watery oviducal secretion enveloped in a thick capsule of the viscous, albuminous secretion of the nidamental gland. From observations of egg laying by female *T. pacificus* in shallow water, it has been suggested that egg masses are deposited on the bottom (Clarke, 1966), however eggs collected from surface horizontal plankton tows suggest that while adhesive egg masses may normally be spawned demersally, they can float secondarily.

The oegopsid *Illex illecebrosus* each produce as many as 10^5 small, nearly spherical eggs distributed in a homogeneous, tenuous, gelatinous mass up to 1 m in diameter. The gelatinous mass secreted by the nidamental gland was often deposited on bottom in tank experiments, but slight water density changes caused them to float (Durward *et al.*, 1980). More recently, however, one female was observed to spawn a free-floating egg mass, midwater in the tank (O'Dor, pers. comm.).

Octopod eggs do not have cases but are surrounded by a chorionic wall produced by the follicular cells (Boletzky, 1974). *Octopus vulgaris* will lay many thousands of eggs in strings of several hundreds (Wells, 1978). Boletzky (1974) described that the "chorion of octopods is drawn into a stalk by which the egg is fastened directly to a substrate or interwoven with other egg stalks to form festoons. The octopod eggs, devoid of protection envelopes, are not abandoned after spawning, but the female broods them (cleaning and manipulating them by suckers and water jets from the funnel) if they are attached to a substrate, or carries them about until the young hatch."

Rate of cephalopod embryonic development is known to be temperature-dependent. Choe (1966a) and Hamabe (1962) reported faster development of eggs in species of squid and cuttlefish as the water temperature became warmer. Similarly, Boletzky (1974) noted that in some species the development period could change considerably. In *Octopus vulgaris*, duration of development changed from less than one month to more than four months with a temperature change from 25°C to 13°C; in *Sepia officinalis* from one and one-half months to three and one-half months for a temperature change from 20°C to 15°C; and in *Loligo vulgaris* from 20 days to 70 days at temperatures from 20°C to 10°C. McMohan and Summers (1971) showed that the rate of egg development of *Loligo pealei* could be modified at any stage of their development by altering the water temperature within a tolerable range. These relationships have important consequences on the reproductive biology of a species, with the entire life cycle timetable being shifted by water temperatures.

There are distinct advantages to this strategy. In many fish and crustacea timing of spawning is critical (Cushing and Walsh, 1976), by this strategy, emerging hatchlings may be provided with temperature regimes suited for growth. Perhaps the more important feature here relates to food availability. By adjusting time for hatching dependent on environment parameters, this strategy probably ensures that the emerging young coincide with the period of plankton bloom. Newly hatched *Loligo opalescens, Illex illecebrosus* and *Todarodes pacificus* planktonic young are encountered in association with planktonic assemblages and are known to feed on planktonic crustacea. Unlike cephalopods that spawn at a fixed season (particularly those in temperate waters), some species such as *Octopus vulgaris* can hatch at any time throughout a major part of the year. Their life cycle strategy is less tuned to the pronounced seasonal variations that species living in the temperate zone have to face. These hatchlings need to accommodate to the prevailing food sources rather than to environmental conditions that change seasonally.

Boletzky (1974) showed that despite differences among egg mass characteristics, ecology and strategy during embryonic development from immature egg through organogenesis to well-differentiated young, is virtually identical among decopods and octopods. As a rule of thumb, species with relatively large eggs produce hatchlings that are very similar to the adult in both form and mode of life. Thus, usually pelagic species produce small eggs and planktonic young and benthic species produce large eggs and benthic young.

Boletzky (1974) noted that all Sepioidea have relatively large eggs and all their newly hatched young, with the exception of one known species, *Idiosepius pygmaeus*, produce benthic hatchlings. This small benthic species, however, produces large eggs but planktonic hatchlings.

Information on Teuthoidea post-embryonic stages is less complete, primarily because they all represent planktonic forms. There have been comprehensive studies on myopsids (Fields, 1965; Boletzky, 1974; Hurley, 1976) which are neritic and relatively easily reared in tanks, while the pelagic oegopsids cannot be reared easily (O'Dor *et al.*, 1980). The myopsid eggs are generally larger than the oegopsid eggs; but overall, Teuthoid eggs are smaller than those of other cephalopods (Boletzky, 1977). The hatchlings emerging from these smaller eggs are all planktonic.

Octopodidae also maintain the egg size/habitat relationship, with an expected variation to the pattern. While the small-sized eggs (2 mm or less) produce planktonic hatchlings and the very large eggs (greater than 10 mm) produce benthic young, the intermediate sizes assume either mode of life, depending on relative egg size (Boletzky, 1974). Planktonic young characteristically have less developed short arms (somewhat similar to the planktonic Teuthoidae), although these are equipped with suckers and have the same prehensile functions as the adult arms. The benthic hatching forms, on the other hand, are more advanced in development and are miniature adults in morphological features.

It is accepted that reproduction is the basic process of maintaining population stability, although the objective of reducing mortality may be fulfilled at any stage of the life cycle. That is, organisms may either counter mortality at reproduction by increasing fecundity or they may reduce reproductive effort and provide the offspring with suitable defences to improve survival.

At first glance, cephalopod strategies seem to be various. On the one hand (primarily in Teuthoids), fecundity is relatively high; as many as 4 x 10^5 eggs have been recorded for *Illex illecebrosus*. Their fecundity by no means matches the millions of eggs produced by some fish, yet their reproductive effort is very high. At the other end of the spectrum some *Loligo* and *Octopus* produce in the range of 1 000 eggs. Even with these low levels of fecundity the reproductive effort apparently is high. Thus, what is common to most cephalopods is that high reproductive effort results in maternal deaths. The significance of this is that the species' continuity is totally dependent on the survival success of the recruits.

A common strategy of organisms with low fecundity is the production of a large quantity of egg yolk. This indeed is true in cephalopods. Additionally, cephalopod egg masses are provided with protective coverings or jelly masses, while some eggs are brooded. Essentially, then, the cephalopod's strategy is to provide the offspring with suitable defences whereby mortality effects are postponed beyond the egg stages.

2.2 Post-Embryonic Stage Strategies

2.2.1 Sepioidea

All hatchlings of five species of Sepiola and Sepietta reared in the laboratory had the common practice of burrowing in the sand during the daytime, evidently to avoid predators (Boletzky *et al.*, 1971). Similarly, hatchlings of *Sepia esculenta* and *S. lycidas* remain buried in the bottom unless actively predating (Choe, 1966). Boletzky *et al.* (1971) described feeding as follows: "After leaving the sand, the animals approach their prey, arms placed together and stretched out forming an elongated cone which points toward the prey... then dart swiftly (propelled by the funnel jet) on the prey and seize it, with their tentacles shooting forward simultaneously. The captured animal is pulled back, to be grabbed instantly by the arms... Sepiolinae usually keep swimming when eating a very large prey, but settle on the bottom (without burrowing) to devour prey of smaller size."

Newly hatched *Sepia officinalis* uses the integument of the ventral mantle surface as a large sucker to attach itself to the substratum. Releasing themselves from attachment, they will attack and capture prey with their tentacles in much the same way as adults (Wells, 1958, 1962). Attacks by *Sepia* are visually guided (Messenger, 1968). These young *Sepia* were found very selective in choice of prey, and chose to attack only *Mysis* during their very early stage of life (Wells, 1962).

The new-born *S. esculenta, S. lycidas* and *Sepiella japonica* start ingesting food within several hours to 24 hours after hatching and readily feed on copepods and *Neomysis japonica* which are considerably larger than themselves (Choe, 1966). Typically, young cuttlefish prey on crab, shrimp or prawns; shrimp and prawns are consumed together with the exoskeleton (Boletzky, 1974). While it is uncertain whether cannibalism occurs among the young, it is known that they do not readily accept dead prey items (Choe, 1966a). In Choe's experiments, *Sepia* exhibited daily growth rates ranging from 6.8 to 16.7 percent of their body weight. *S. esculenta* had a daily feeding rate of 11.0-39.4 percent during the first 31 days after hatching, and their corresponding conversion efficiency ranged from 9.0 to 71.0 percent.

2.2.2 Teuthoidea

Few laboratory observations have been made of planktonic teuthoid hatchlings. Among other experiments, Boletzky (1974) reared *Loligo vulgaris* to 45 days from hatching. Fields (1965) successfully maintained *Loligo opalescens* up to ten days from hatching, and Hurley (1976) the same species up to 100 days. Newly hatched *L. opalescens* were described as active and agile, and soon after hatching they assumed their planktonic mode of life by swimming upward and toward light (Fields, 1965). During their early planktonic life, they remain immediately below the water surface, and Bigelow and Leslie (1930) encountered them in the upper 15 m of water. Okutani and McGowan (1969) similarly found them most common in the upper 40 m. Within a few days after hatching, young squid readily attack prey as large as themselves, such as copepods, small mysids, *Artemia* and larval crustacea were readily attacked and consumed (Boletzky, 1974; Hurley, 1976). Choe (1966a) observed newly hatched *Sepioteuthis lessoniana* start feeding within a few hours to 24 h. When attacking, young squid were visually guided, similar to behaviour described for cuttlefish by Messenger (1968), and were not extremely selective as to the prey type, as were the cuttlefish.

Fields (1965) described some observations on young *L. opalescens* in Monterey Bay, California. Distribution patterns show they join the surface assemblages which are constituted mainly of diatoms, dinoflagellates and larvae and juveniles of copepods, euphasiids and decapod crustacea. The young squid are thought to feed upon larvae and juvenile crustacea while their chief predators are ctenophores, arrow worms and siphonophores. Both predator and prey go deeper as they grow, and the young squid, together with the plankton, are transported and distributed by coastal currents.

It is uncertain whether planktonic young squid are cannibalistic. Although they have often been observed to attack each other in tank experiments, this is attributed to lack of suitable food organisms in sufficient quantity (Boletzky, 1974).

Quantitative studies by Choe (1966) showed that daily growth rates estimated for young *Sepioteuthis lessoniana* of 0.5 to 6.0 mm mantle length were 4.1-5.9 percent for mantle length and 7.1-10.7 percent for body weight. *Loligo opalescens,* a few days after hatching, fed on prey ranging from one-quarter to about twice their mantle length, with an apparent preference for larger prey (Hurley, 1976). Their daily feeding rates varied between 35 and 80 percent of body weight.

In contrast to the Myopsidae, experiments conducted on Oegopsidae are very limited, primarily because these pelagic forms are difficult to maintain or breed in captivity. Most extensively studied oegopsids are the Japanese *Todarodes pacificus* (Hamabe, 1962) and *Illex illecebrosus* (O'Dor, Balch and Amaratunga, 1981) of the northwest Atlantic. These two ommastrephids have been successfully observed under experimental conditions as well as extensively studied under field conditions.

Newly hatched Ommastrephidae bear a characteristic form which has been summarized by Roper and Lu (1979): "The larvae of ommastrephid squids are characterized by the fusion of the two tentacles... Larvae bearing the tentacles fused into a proboscis are termed the Rhynchoteuthion stage, a general designation that carries no nomenclatorial status. Chun (1903) originally recognized the form and described it as *Rhynchoteuthis.*"

Newly hatched *Todarodes pacificus,* 0.74-1.02 mm long, were unable to swim clear off the bottom and tended to crawl, clinging to the bottom in laboratory experiments (Hamabe, 1962). Soon after, however, they are believed to swim up to the surface layers of water. In field surveys, Rhynchoteuthion stages have often been encountered in the surface region of the water to depths of 50 m. They are also known to retain the typical Rhynchoteuthion stage until the animals are about 15 mm in length, which is estimated at a minimum of two weeks of post-larval development (Hamabe, 1962). On the basis of field samples, newly hatched stages were assumed to occur in temperatures warmer than 16°C (Shojima, 1972) and high salinity ranges. Such hydrographic features are characteristic of the water masses of the Tsushima current and Kuroshio region (Okiyama, 1965).

A very similar ommastrephid is the northwest Atlantic short-finned squid, *Illex* illecebrosus. Until recently, laboratory experimentations on this species were few; but Roper and Lu (1979), from field samples, were able to characterize larvae and juveniles ranging from 1.5 mm to 18 mm mantle lengths. Subsequently, surveys of the oceanic water masses of the northwest Atlantic, extending from the continental shelf to the Sargasso Sea (Amaratunga, Rowell and Roberge, 1980) and laboratory induced spawning (Durward *et al.*, 1980; O'Dor, Balch and Amaratunga, 1981) have improved our understanding of their life cycle.

The first recorded spawning of *Illex* in capivity in 1979 (Durward *et al.*, 1980) and subsequent years, have provided descriptions of spawning habits, embroyonic development, and early larval forms (O'Dor, Balch and Amaratunga, 1981). Rhynchoteuthion stage larvae emerge from *I. illecebrosus* egg masses in about 11 days at 13°C. The minimum temperature at which eggs will develop normally is between 10°C and 13°C, but often development fails below 12°C (O'Dor *et al.*, 1981). The Rhynchoteuthion hatchlings, about 1.1 mm in mantle length, survived in tanks to a maximum of 10 days on the yolk reserves without exhibiting any predatory activity. The hatchlings were unable to swim but were able to scoot about at the bottom of the tank for a day or more. It is suggested that in nature they spend this period within the gelatinous mass (Durward *et al.*, 1980). In these experiments the Rhynchoteuthion was later able to move up the water column by rapid mantle contractions. Transition to the juvenile form occurs when the proboscis divides into two tentacles at 8 mm to 10 mm mantle length. Offshore surveys between February and May since 1979 have produced several thousand specimens ranging from Rhynchoteuthion stages up to 120 mm mantle length (Amaratunga, Rowell and Roberge, 1980). These distributions range geographically from waters off Cape Hatteras, North Carolina, to Grand Banks, Newfoundland, and are most abundant in the upper 100 m of the landward skirt of the Gulf Stream at temperatures from 14.3°C to 16.3°C and salinities from 35.8 percent to 36.3 percent (Amaratunga, Rowell and Roberge, 1980). Near-surface bongo hauls resulted in the capture of many early stages, conforming with laboratory observations by O'Dor, Balch and Amaratunga, 1981).

Thus, we have seen that in the Teuthoids the newly hatched myopsids and oegopsids have very similar life style strategies. Although the eggs may have been either benthic in one group and pelagic (or associated with pelagic waters) in the other, we have noted that hatchlings soon assume a common planktonic role. The main difference apparent at the hatchling stage is perhaps related to the shallower habitat of the myopsid, where the myopsid hatchlings have developed more adult-like features than the ommastrephids.

Many teuthoid young are commonly encountered in relatively warm environments, and are often associated with more productive areas of water masses, such as areas of upwellings and interphase zones of water currents and the ommastrephids discussed and also *Loligo* sp. occur in these ecosystems.

Within the planktonic ecosystem, these squid are active predators feeding voraciously but selectively. Generally, the predominant prey types are larval stages and the small-sized crustacea, such as copepods, amphipods, mysids and euphausiids. Among the early stages of *I. illecebrosus* encountered in the 1979 offshore survey off Nova Scotia, only 13 percent had gut contents (Amaratunga, 1980). Interestingly, more than 50 percent of these animals had squid fragments in the contents, suggesting cannibalism can occur.

2.2.3 Octopoda

Young (1977) demonstrated that from many features such as the nervous system, statocyst, photosensitive vesicle other than the number of arms, sepiods and teuthoids are closer to each other than either are to octopods, however similarities between decapods and octopods soon become apparent when we consider life-style strategies.

The newly hatched octopods, which directly assume the benthic form of life, usually resemble the adult in appearance. Predation behaviour is similar also, but they eat relatively more and grow faster. Those hatchlings that assume a planktonic phase are not totally adult-like. *Octopus vulgaris*, for instance, which spends perhaps as much as three months in the plankton in the northernmost areas of its range in the northeast Atlantic, develops adult-like characteristics during the planktonic phase. At recruitment to the planktonic phase, their arms are relatively short but equipped with suckers for prehensile activity. The arms grow in relative size and the animals grow from about 3 mm to 10 mm in total length to resemble adults by the time they settle on the sea bed (Wells, 1978).

Planktonic octopods use the visual attack methods described for *Sepia* (Messenger, 1968) by shooting forward and seizing the prey directly with all arms (Boletzky, 1974). They feed predominantly on crustacea such as crab, shrimp and lobster but may also consume molluscs. In laboratory conditions, they have shown cannibalistic attacks. They capture live prey preferentially, but can become scavengers on occasion. Newly settled octopods fed on shrimp and crab meat and later on small, live crabs, showed a tenfold average size increase in 40 days at 25°C (Itami *et al.*, 1963; Wells, 1978). Mangold-Wirz and Boletzky (1973) found food intake and growth fell with increasing temperature. For smaller sizes, metabolic rates were high but the average conversion efficiency for crab meat diets was also high at 50 percent (Wells, 1978)

2.3 Juvenile and Adult Strategies

2.3.1 Sepioidea

Ecologically, cuttlefish are generally inshore and neritic species, spending much of their lives near or on the sea bed. They are absent from waters of the New World, being found in the eastern Atlantic from northern Europe to South Africa, in coastal areas of the Indian Ocean, and in the western Pacific from Japan to Australia (Voss, 1973).

Apart from the genus *Octopus*, only the cephalopod genera *Sepia* and *Sepiella* have more than one hundred representative species (Voss, 1973). *Sepia officinalis* is the most important cuttlefish occurring in the coastal regions of Europe and Africa. *S. officinalis* juvenile and adult life stages are spent on the sea bed at depths ranging from 0 m to 250 m (Mangold-Wirz, 1963). They are nocturnal predators, spending daylight hours partially buried in sand or gravel, and night-time hours swimming. During the day, they adopt a camouflage strategy relying on chromatophores and iridophores for concealment in the substratum. During the night they change their buoyancy and swim in search of prey. Full development of the brain, eyes and statocyst (Young, 1977) Reflect an active shallow-water life dependent on sight. Similarly, the nervous system with giant fibres is fully developed to achieve fast swimming and rapid manouvres.

S. officinalis prey on fast-moving animals, such as prawns, smaller cuttlefish and fish. Prey attack is visually controlled (Messenger, 1977), and prey seizure is by ejectile tentacles which carry prehensile suckers on their terminal club. *S. officinalis* also feeds on less active organisms. When preying on slow-moving animals such as crabs, the attack once again is visually controlled, but prey seizure may be accomplished with the arms without the use of tentacles.

Messenger (1977) described three phases of attack for tentacular seizure. The cuttlefish first makes visual contact and aligns itself to face the prey directly; it then positions itself to an "attacking distance" and finally strikes by tentacle ejection. This efficiency, mediated through the optic system and central and peripheral nervous systems, is also matched by specialization of suckers on the tentacular club (Nixon and Dilly, 1977). These are adapted to grasp at lightening speed; chemoreceptors around them transmit information about the prey, before it reaches the mouth. Tentacular attacks have had very high success rates in the laboratory (Messenger, 1968): 90 percent on first attack and 100 percent on the second. Experiments, however, have shown that the success of the predators' attacks per prey encounter diminishes when the prey occurs in a school (Neill and Cullen, 1974).

S. officinalis uses poison to kill crustacea (Bidder, 1966). The toxic secretion of the posterior salivary gland acts on crustacean prey only after an incision has been made. In *Sepia* (as with squid), large chunks of flesh and skeleton are believed to be swallowed quickly so that no external digestion can take place.

Studies on *Sepia esculenta* have shown live prey is preferred to dead material (Choe, 1966a). While juveniles accepted dead food, their normal growth rates decreased dramatically. The duration of a meal (described in this instance as the time of capture of food to the time when stomach and caecum return to the hunger condition) was estimated for both *Sepia* and *Octopus* to vary between 15 and 20 hours according to water temperature (Bidder, 1966). Although experiment methods were not reported, these timings were assessed to be reasonable, based on enzyme deployment in the digestive process. In *Sepia,* the hepatic enzymes are responsible for the initial gastric digestion; and while liver cells are passing through absorptive and excretary phases, no hepatic enzymes are available for gastric digestion. Thus, when a meal first induces hepatic enzyme secretion, and secretion is exhausted, the next digestive process can only start when the liver is freed from the function of absorption and subsequent excretion. Therefore, if *Sepia* consumes a substantial meal, the digestive processes alone will require that no further meal is taken again that day. If the meal sizes were small, it is likely that feeding will continue until the daily meal requirement is obtained.

2.3.2 Teuthoidea, Myopsidae

Myopsidae are neritic species, and the common genus *Loligo* is encountered in all the ocean regions of the world. Their habitat ranges from subtidal to about 200 m at the continental shelf break. Juvenile and adult *Loligo* may be characterized as perpetual swimmers and active predators. Seasonally, they exhibit migration patterns, which could represent a north-south orientation in relation to prevailing temperatures or it could represent a local inshore-offshore orientation. They may also have a diel vertical cycle.

For all its activities, *Loligo* has a very well-developed brain and sense organs and a giant nerve fibre system (Young, 1977). In *Loligo* and *Sepia* brain and statocyst development have been described as similar in many respects as a result of their similar habitats; but in other respects, *Loligo* and ommastrephid squid resemble each other much more closely than *Sepia.* Their active predatory life style is dependent on an efficient visual sensory system, much in the same way as *Sepia. Loligo,* in contrast, maintains a more pelagic form of existence, requiring continuous swimming, for which purpose the giant nerve cell system is better developed than in any other caphalopod (Young, 1977).

Juvenile and adult predatory behaviour by *Loligo* has been described for many species by various authors. The behaviour scheme for all observed *Loligo* spp. may be generalized as an active, visually controlled attack, usually on fast-moving prey, such as crustacea and fish and quite often others of their own kind. The animal maintains swimming motion by jet propulsion and undulation of the tail fin. As soon as the prey is detected, during laboratory experiments, it is noted that *L. opalescens* demonstrates excitement by displays of colour rapidly racing over the mantle (Fields, 1965). The animal then immediately prepares for attack by approaching the prey. The three phases of attack described for *Sepia* by Messenger (1968) also seem to apply to *L. opalescens* (Hurley, 1975) and young *L. vulgaris* (Worms, 1979).

Fields (1965) observed for *L. opalescens* that captured prey are held and manoeuvred for feeding by the arms. Smaller prey are brought immediately to the mouth with the arms held in a cone-like arrangement, and biting and swallowing proceed immediately. While eating, the squid may continue to attack and capture more prey, now using only the tips of the arm cone to receive new food brought in by the tentacles. Often, shrimp enclosed in the arm cone remained active and in some cases clambered out between arms. They, however, were recaptured by the squid disengaging an arm for the purpose. Fields found that all of these activities were remarkably well coordinated without mutual interference.

Loligo are able to seize large prey, usually at a maximum size slightly smaller than their mantle length. Once the prey (fish or squid) is seized, Bidder (1950) states that in *L. vulgaris* the procedure is always the same. If it is a fish, it is held obliquely until the head is bitten off and dropped. The trunk of the fish is then held horizontally, anterior end toward the beak and the tail projecting outward into the arm cone. The squid then make a series of transverse bites until the fleshy parts are all consumed. Bidder found that *Loligo* rejected the fish alimentary system, the vertebrae and caudal fin. The food is bitten off in chunks as large as the beak can handle and swallowed with the help of the radula and probably the salivary secretions.

. Bidder (1950), investigating the digestion mechanism of four European loliginids, viz *Loligo forbesiy, L. vulgaris, Alloteuthis media* and *A. subulata,* noted that food is rapidly swallowed and a preliminary phase of digestion in the stomach concludes in the caecum. In *Loligo,* unlike in *Sepia,* the liver is freed from the function of absorption and the whole digestive mechanism is adapted to the life of a continually swimming animal. The segregation of gastric and caecal digestion are particularly well fitted to allow continuous feeding, without interfering with the digestion of an earlier meal.

Digestion rates are very rapid in *Loligo,* and qualitative estimates are from four to six hours (Bidder, 1966). In the normal ambient temperature range (13°C - 20°C), the rate of digestion is not affected, however size of squid and type and size of meal may affect rates of complete digestion. In a field study of *L. opalescens,* relatively small-size (average 87 mm mantle length, compared to adults up to 180 mm), sexually immature animals were analysed for chronology of digestion of food (Karpov and Cailliet, 1978). Meal size as a percentage of body weight showed that no digestion occurred until after two hours, but after five to seven hours, digestion was complete. This represented an average digestion rate of 0.29 percent dry body weight per hour, and a stomach emptying time of 6.6 hours.

Prey preference varies among species as well as within species. Among the loliginid species obvious factors, such as geographic variation, result in considerable variation in the prey species consumed. Similarly, age and maturity within a species results in prey variations. At this point, let us consider the predation patterns of two of the most extensively studied species: *Loligo opalescens* and *Loligo pealei.* These two species are found in the Pacific Ocean and Atlantic Ocean, respectively.

Although squids swallow large chunks, often stomach contents are difficult to identify, since especially when fish are consumed, *Loligo* discards heads, backbones and tails. Similarly, other hard tissue which are invaluable for identification purposes are often not available. Additionally, soft tissue breakdown is very rapid as digestion begins (Wallace, O'Dor and Amaratunga, 1980). When crustacea are consumed, however, distinctive exoskeleton fragments, such as eyes, mandibles, rostrum and carapace are available for prey recognition. Likewise, squid in stomach contents are identifiable from beaks and characteristic features visible in the large chunks usually consumed.

The major studies where prey preferences of *L. opalescens* were evaluated by Karpov and Cailliet (1978) and Fields (1965). Table 1 shows a list of prey types. Karpov and Cailliet found *L. opalescens* fed mainly on crustacea and to a much lesser degree on fish, cephalopods, gastropods and plychaetes. In the crustacean component, euphausiids and copepods dominated the diet; but mysids, megalops larvae, cumaceans and amphipods represented important percentages in certain locations. Fields, on the other hand, noted that food of each stomach analysed commonly contained only one prey type, and only in a few cases were two or three of these types found together. Euphausiids and mysids, in that order, were the predominant prey type in these studies as well, while amphipods and megalops larvae were present less often.

Considering relative importance of prey type between large (101-180 mm mantle length) and small (21-100 mm mantle length) *L. opalescens*, Karpov and Cailliet found that both groups predominantly fed on euphausiids, *Euphausia pacifica* and *Thysanoessa spinifera*. The overwhelming large numbers of euphausiids eaten (94.8 percent of the identified cases in the small squid, 98.4 percent in the large squid) rendered the other prey by numbers relatively insignificant. In relation to depth, squid captured deeper in the water had consumed a larger number of euphausiids and copepods than those nearer the surface. Cephalopods and fish constituted important components in the surface squid. There was generally very little difference between male and female feeding habits.

In the spawning schools of *L. opalescens*, Fields (1965) found 75 percent of the animals that had fed had cannibalized, 21.5 percent had consumed fish, and 7 percent had consumed crustacea. He noted that in squid caught among fish schools the percentage of meals with fish increased only to 30 percent. Then, cannibalism decreased to 10 percent while crustacean and polychaete meals increased to 73 percent and 4.8 percent, respectively. (These meals reported sometimes contained more than one prey type; as a result, total percentage exceeded 100 percent. Each constituent prey type was then given a percentage point; as a result, total percentage might exceed 100 percent).

Table 1

List of confirmed prey items found in juvenile and adult *L. opalescens*, Combined data from Fields (1965) and by Karpov and Cailliet (1978)

Prey type		Degree of abundance [a]
Crustacea:		
Euphausiacea	- *Euphausia pacifica*	Abundant
	- *Thysanoessa spinifera*	Abundant
Copepoda	- *Calanoid* sp.	Present
Mysidacea	-	Common
Megalops	-	Present
Natantia	- *Sergestes* sp.	Present
Cumacea	-	Present
Amphipoda	- *Jassa* sp.	Present
Ostracoda	-	Present
Unidentified crustacea		-
Cephalopoda:		
	- *Loligo opalescens*	Common
	- *Gonatus* sp.	Present
	- *Rossia pacifica*	Present
Unidentified cephalopods		-
Gastropoda:		Present
Radiolaria:		Present
Polycheata:		Present
Fish:		
	- *Engraulis mordax*	Common
	- *Sebastes sp.* (juveniles)	Present
	- flatfish (unidentified)	Present
Unidentified fish.		-

[a] Relative abundance estimated from quantitative statements made by authors

Few authors have reported feeding habits of *Loligo pealei* (Verrill, 1882; Williams, 1909; Vovk, 1974; Vinogradov and Noskov, 1979). Generally, these authors confirm that *L. pealei* feed primarily on crustacea, fish and fellow squid (Table 2) in varying proportions.

Prey items changed in relation to size or age of *Loligo*. Williams (1909) and Vovk (1974) noted juvenile *L. pealei* (ranging 75-100 mm in mantle length) fed primarily on planktonic crustacea which included copepods and larval forms. Vovk also found some euphausiids and decapods, while a very small proportion of the diet showed fish and squid as well. Euphausiids became the major food item in the diet, and both fish and squid increased in proportion as the *L. pealei* increased to 160 mm mantle length.

Vinogradov and Noskov (1979) found that the smaller squid (80-150 mm mantle length) fed in the proportion of 40 percent crustacea, 40 percent fish and 20 percent squid. At mantle lengths greater than 160 mm, their preference changed to larger prey such as fish and squid, while euphausiids and other prey items decreased to less than 12 percent in volume (Vovk, 1974). Cannibalism became the most important predation pattern in the larger squid, and Williams (1909) claimed that it was not uncommon to find in the stomachs of *L. pealei* chunks from individuals presumed to be of the same size as the predator. In squid between 160 mm and 300 mm, the proportions noted for crustacea, fish and squid were 18 percent, 61 percent and 21 percent, respectively (Vinogradov and Noskov, 1979).

Prey types were also noted to vary by area and season (Vinogradov and Noskov, 1979). For example, in August and October small squid on Georges Bank fed mainly on crustaceans, whereas in November the diet almost entirely consisted of silver hake. Large squid in the same area and times, on the other hand, consumed an increasing amount of fish and squid as the season progressed.

Diurnal patterns of feeding periodicity are apparently observable according to Vovk. In the autumn months, these species showed maximum stomach fullness in the evening from 16.00-20.00 h. However, Vinogradov and Noskov obtained no clear diurnal pattern although the most intensive feeding by large squid occurred again during the evening between 18.00-20.00 h. When interpreting these data, Lange (1980) suggested that *L. pealei* may have differential vertical migration by size, where larger individuals remain at the bottom at night while the smaller ones move up the water column to feed on plankton.

Table 2

List of reported prey items found in *L. pealei*

Prey type	Degree of abundance[a]
Crustacea:	
Gammarids	Present
Euphausiids	Abundant
Crabs	Present
Shrimp	Common
Lobster	Rare
Mysids	Common
Crab Larvae	Present
Copepods	Present
Unidentified Crustacea	-

Table 2 (continued)

Prey type	Degree of abundance[a/]
Cephalopoda:	
Loligo pealei	Common
Fish:	
Merluccius bilinearis	Common
Mackerel	Common
Alewife	Present
Atlantic saury	Present
Herring	Common
Lantern fish	Present
Sagittas	Present
Fish larvae	Present
Unidentified fish	-

a/Relative abundance estimated from quantitative statement made by the authors.

2.3.3 Teuthoidea, Oegopsidae

The group Oegopsidae contains the oceanic squid found mainly beyond the edge of the continental shelf; however, they are highly diverse in range and habitat (Voss, 1973). The classification list (Table 1 of Appendix) shows the large number of families within this group; however, economically important species are mostly ommastrephids.

Ommastrephids, although they are considered to be oceanic squid, often have many species that spend a period of their life cycle (sometimes a large proportion of their life) on the shelf areas extending even into inshore waters. Some of the most prominent and commercially important species, *Todarodes pacificus, Illex illecebrosus, I. argentinus,* and *I. coindetiy,* show examples of such distribution patterns. Perhaps because of their adaptations to habitats ranging from shallow waters to the continental shelf edges, ommastrephids have sometimes been classified together with *Loligo.* There are indeed many similarities in the brain and sense organ systems between *Loligo* and the two most important ommastrephids: *Todarodes* and *Illex* (Young, 1977). Environmentally, *T. pacificus* differs primarily in that this species extends its distribution to as much as 1 000 m (Clarke, 1966) and *I. illecebrosus* which has been encountered as deep as 750 m (Amaratunga, Kawahara and Kono, 1979). Thus, Young (1977) noted that the photosensitive vescicles around the optic tract of these ommastrephids were much better developed than in *Loligo.* It is suggested that the photosensitive vescicle provides a system for measuring light intensity and functions as a monitor for daily and seasonal changes of illumination. In *I. illecebrosus* it has been demonstrated that photoperiodicity influences sexual maturation patterns (Durward *et al.,* 1980).

Ommastrephids, just as *Loligo,* are perpetual swimmers and active predators, and are very similar in life style characteristics. They have seasonal migrations and more pronounced diurnal migrations than those reported for *Loligo.* This life style in turn is supported by a very similar, well-developed giant fibre system, an extremely efficient visual sensory system, and statocysts (Young, 1977).

Observations on juvenile and adult food and feeding in ommastrephids are not as extensive as for *Loligo*. Much of the information has resulted from studies on *Illex illecebrosus* (Squires, 1957; Mercer and Paulmier, 1974; Amaratunga, Kawahara and Kono, 1979; Ennis and Collins, 1979; Vinogradov and Noskov, 1979; O'Dor *et al.*, 1980), while related reports on *Todarodes pacificus* and other species are incidental. *I. illecebrosus* will be considered here as a representative of the ommastrephids, although not all the following observations are totally applicable to all other species of the family.

Adult *I. illecebrosus* (about 200 mm mantle length), held in captivity, usually remain in a relatively tight school (O'Dor *et al.*, 1980). They show food preferences, feeding readily on a variety of small fish and shrimp, including capelin, herring, mackerel, smelt, salmon smolt and sand shrimp, but rejecting others such as eels and crabs after capturing them. They also showed a size preference for prey when tested with a size range of herring. The upper limit to the size of prey which they attacked was roughly equal to their mantle length, but they were relatively unselective below this limit.

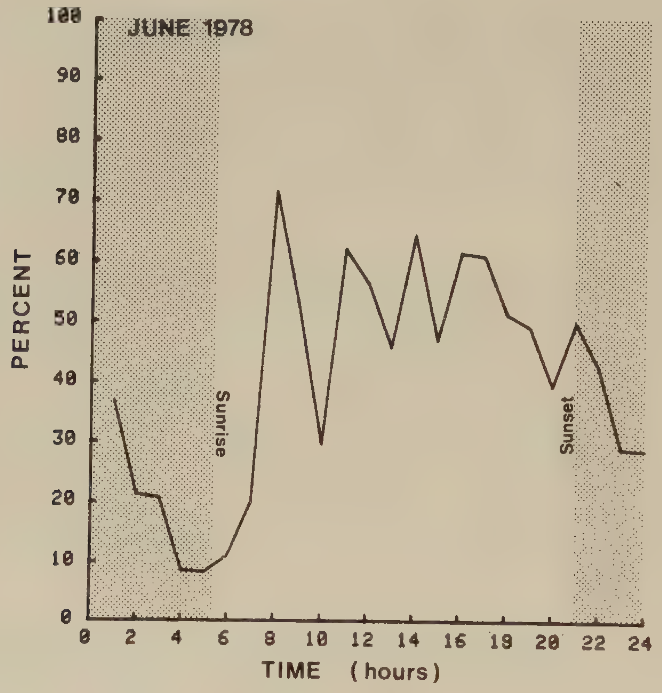
When live fish were singly offered to the school of squid, the largest squid generally fed first, darting out of the school to capture the fish and then quickly returning to the school. At this stage, smaller squid which attempted to capture prey were attacked by the larger squid. Not until the larger squid had captured sufficient prey, or was satiated, were the smaller squid in the school allowed to feed. The visual method of predation by individual squid described for *Loligo* (Bidder, 1950) applied here. However, observations were difficult when a school of fish was introduced to the squid, and all squid appeared to feed then. It is very probable that the success rate of prey capture depended on prey school size. Squid (and cuttlefish) prey captures success decreased in an experiment where prey school size was increased from one fish to 6-20 fish (Neill and Cullen, 1974).

Similarly to *Loligo*, *I. illecebrosus* may capture a single large prey or a large number of small-sized prey per meal. When feeding on fish, they typically oriented the prey within the arm cone and methodically consumed the fleshy parts bite by bite. These squid were also selective and consumed mainly the fleshy parts of the fish, discarding the head, viscera and vertebrae as did *Loligo*. Again, when preying on crustacea they tended to consume them in entirety, inclusive of the exoskeleton. Cannibalism was observed among captive squid that were not adequately fed (O'Dor *et al.*, 1979), and predation took place upon squid that were smaller than themselves. Squid were totally consumed, usually in chunks 2-5 mm in size.

Ingested material is stored and digested in the stomach, the digestive process being very similar to that described for *Loligo* by Bidder (1950). The sequential process of tissue breakdown or digestion was described by Wallace *et al.* (1981). Food chunks gradually turned into a thick, gooey mass which in turn thinned out to a clear fluid. The estimated time for digesting an average meal of 6.4 percent (3-11 percent range) of body weight at 10°C was 12-13 hours. Meals in Boucher-Rodoni's (1975) experiment ranging from 5 to 10 percent body weight at 10°C took 10-12 hours. In other studies, meals as large as 15 percent of body weight were thought to be common; the largest meal size seen was 25 percent of body weight (O'Dor *et al.*, 1980). It is believed that larger meals take longer to digest (Wallace, O'Dor and Amaratunga, 1980), and O'Dor *et al.* (1980) have observed *Illex* skip regular (daily) feeding after taking a large meal; food was still visible through the mantle 24 hours later. In general, however, sustained feeding rates are thought not to exceed 10-15 percent of body weight in adult *I. illecebrosus* about 200 mm mantle length, and feeding takes place daily.

Field studies also show *I. illecebrosus* mainly feeding once a day. Amaratunga, 1980a) observed diurnal feeding patterns in two consecutive years of study. The percentage of squid which had recently fed increased dramatically shortly after sunrise (Figure 1) for both juveniles (150 mm mantle length) recently arrived on the continental shelf in spring and autumn populations of adults close to maturity (250 mm mantle length). Apparently, squid move up the water column to feed during the pre-dawn hours. The numbers of recently fed animals gradually decreased as the daylight hours progressed, during which time digestion was assumed to be in progress. Bradbury and Aldrich (1969) reported that squid in captivity fed before daybreak, while other field studies have also shown diurnal feeding periodicy (Vinogradov and Noskov, 1979).

In *I. illecebrosus*, seasonal variations in feeding patterns and prey preferences are related to age and show a definite seasonality in distribution. Following early stages of life associated with the northern boundary of the Gulf Stream, juveniles 100-150 mm mantle length first arrive on the continental shelves of Nova Scotia and Grand Banks in spring (May/June) (Squires, 1957; Amaratunga, 1980). Fedulov and Amaratunga (1981)demonstrated that sea temperature was related to the date of immigration to the Scotian shelf; however, this strategy is apparently more related to availability of preferred prey.



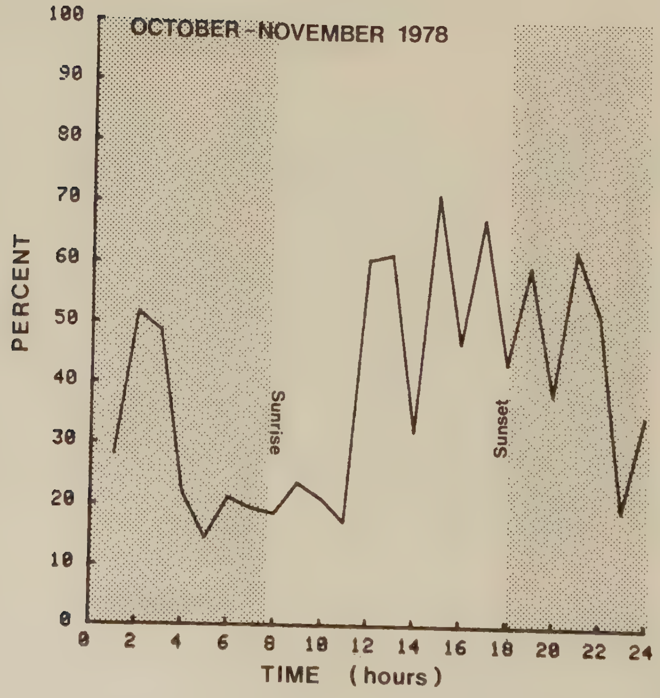


Figure 1 Percentage of "recently fed" animals in samples plotted through time of day, showing diurnal fluctuations of feeding activity during June and October-November, 1978

Amaratunga (1980) observed that squid first arriving on the Scotian shelf in spring of 1978 and 1979 exhibited active feeding (Figure 2). Their diet, which consisted exclusively of euphausiids, coincides with the seasonal availability of *Meganyctiphanes norvegica, Thysanoessa inermis* and *Th. rashii* on the shelf. Feeding frequency decreased between May and late July. Seasonal variations in euphausiids corroborate this. The second year class of *Meganyctiphanes norvegica* spawn and die in June-July (Hollingshead and Corey, 1974), while in *Thysanoessa* a similar spawning stock mortality is known from April to the latter part of May (Kulka and Corey, 1978; Kulka, 1977). In *Thysanoessa inermis*, post-spawning mortality in fact represents a depletion of 30-40 percent of the adult population (Kulka, 1977). The seasonality of these mortalities provides a striking correlation between food limitation and decrease in squid feeding. The period of decreased feeding coincides with a change in prey types to include crustacea, squid and fish, probably implying a switch from the now less available euphausiids to more accessible prey; a phenomenon observed in fishes. A subsequent increase in feeding activity ensued; fish and squid increasing in importance as prey components, although crustacea still constitute a major proportion of the diet. At the same time, rapid growth of the next year class leads to replenishment of euphausiid size classes suitable for squid consumption (Kulka and Corey, 1978).

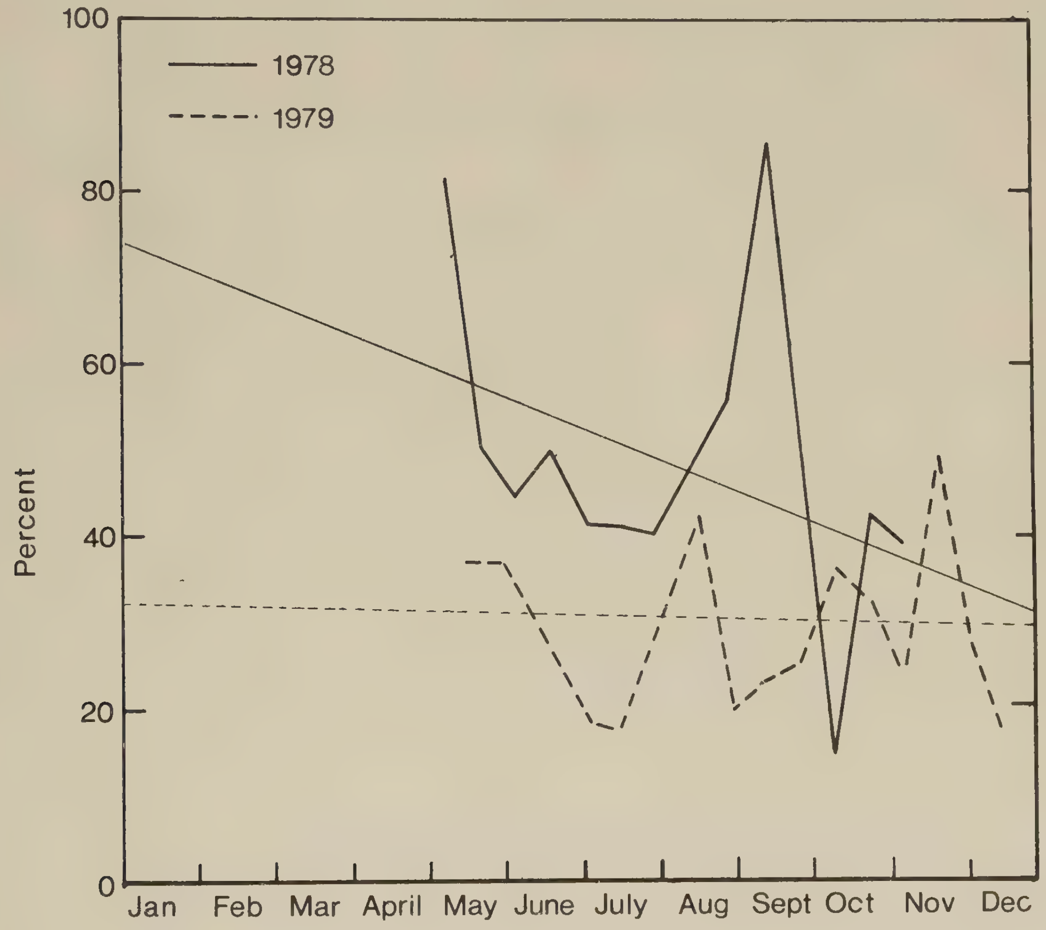


Figure 2 Seasonal variation of the percentage of animals that had recently fed in the samples of *Illex illecebrosus* from the Scotian shelf. Linear regressions are:

1978: percent = 74.9 - 0.833 (week)
1979: percent = 32.2 - 0.053 (week)

Increased cannibalism and fish predation in the autumn are probably related to the fact that squid are very much larger (Amaratunga, 1980a) and are preying on alternative size-related food types. Similar progression of prey types and size-related food preferences have been observed for *I. illecebrosus* (Squires, 1957; Vinogradov and Noskov, 1979) and *Loligo* species (Vovk, 1974; Fields, 1965).

In conclusion, the progression of predation from crustacea to fish and squid (Figure 3) may be attributed to both availability and size-related prey preference. In the early stages, crustacea and later fish and other squid are important. It is unclear as to why the fish component was relatively unimportant in *I. illecebrosus* from the Scotian shelf. Fish may in some years constitute an important proportion of the prey (Squires, 1957; Ennis and Collins, 1979), and indeed squid are known to prey on inshore herring and mackerel stocks in Nova Scotia. It is probable that fish are less available in some years, but we do know that cannibalism is a widespread phenomenon among cephalopods. Table 3 shows a list of prey types from Amaratunga (1980a).

Table 3

List of confirmed prey items found in juvenile and adult *Illex illecebrosus*

Prey type		Degree of abundance
Fish:		
	Myctophum punctatum	Common
	Ceratoscopelus maderensis	Present
	Notolepis rissoi	Present
	Urophycis chesteri	Present
	Merluccius bilinearis	Common
	Gadidae	Common
	Macrouridae	Present
	Unidentified fish	–
Crustacea:		
	Euphausiids (*Meganyctiphanes*	Abundant
	sp. and/or *Thysanoessa* sp.)	Abundant
	Unidentified euphausiids	–
	Candacia armata	Present
	Euchaeta norvegica	Present
	Unidentified copepods	Present
	Parathemisto sp.	Present
	Unidentified crustacea	–
Cephalopods:		
	Illex illecebrosus	Common
	Gonatus fabrici	Present
	Histioteuthidae	Present
	Unidentified cephalopods	–

Table 3 (continued)

Prey type	Degree of abundance
Miscellaneous:	
Pteropods	Present
Chaetognaths	Present
Unidentified prey items	-

2.3.4 *Octopus*

Ecologically, Octopodidae are bottom-dwelling species usually limited to the neritic province. They are found in various parts of the world; however, many of them are more commonly found in the tropical and temperate waters. Some are gregarious, while many others demonstrate individual territorial activity (Voss, 1973). Voss (1973) also states that some octopods show seasonal breeding migrations from the outer shelf area to inshore areas and back, while others remain in one locality.

The genus *Octopus* carries more than 100 species, and along with *Sepia* sp. and *Sepiella* sp. account for close to 50 percent of all the described cephalopod species. *Octopus vulgaris* is perhaps the most important, and along with *O. macropus* is a widely distributed species occuring throughout the tropical and temperate oceans of the world.

Juvenile and adult *O. vulgaris* inhabit waters from 0-100 m (found to depths of 250 m), living in holes and crevices on the sea bed, and they occupy the same crevice "home" for long periods of their life (Nixon and Dilly, 1977). Although they are opportunistic feeders ready to feed at any time, they commonly forage nocturnally (Wells, 1978). Wells (1978) described that food is gathered by touch; sensitive tactile and chemical receptors in the arms permit very selective predation. Thus octupus moves around "feeling into cracks and under stones; from time to time it moves swiftly across to gather something that it has detected with one of the arms." The octopus will capture and kill several prey before eating them back at their home.

The prey are mainly crustacea, such as crabs and molluscs. Crabs are paralysed in less than 30 seconds (Nixon and Dilly, 1977) and killed by a toxic secretion "cephalotoxin" produced by the posterior salivary gland. In molluscs they bore a hole through the shell with the radula and inject them with poison.

3. TROPHIC RELATIONSHIPS

Due to the great variety of cephalopods, general statements on trophic relationships are very difficult to make. For example, Hardy's famous feeding relationship study of the North Sea herring (Hardy, 1924) demonstrates the extreme complexity a food web can attain. Vovk (1974), illustrating the trophic position of *Loligo pealei* in the ecosystem, listed 67 predator and prey organisms. Important trophic relationships were indeed presented, but not only were the numbers extremely large, the data were misleading because of the wide size range and distribution being considered. Thus, in the present exercise we do have to generalize for the obvious reason of simplicity.

3.1 Egg and Post-Embryonic Stages

The cephalopod eggs may be encountered from shallow benthic subtidal waters to the base of the continental slopes, and from neritic to oceanic pelagic free-floating forms; thus, their predators vary considerably. Accordingly, the number of eggs and life strategies also vary considerably. Usually the pelagic forms (usually oegopsids) produce a reasonably large number of eggs enveloped in a gelatinous protective covering. The gelatinous cover may afford protection, especially against microbial attack

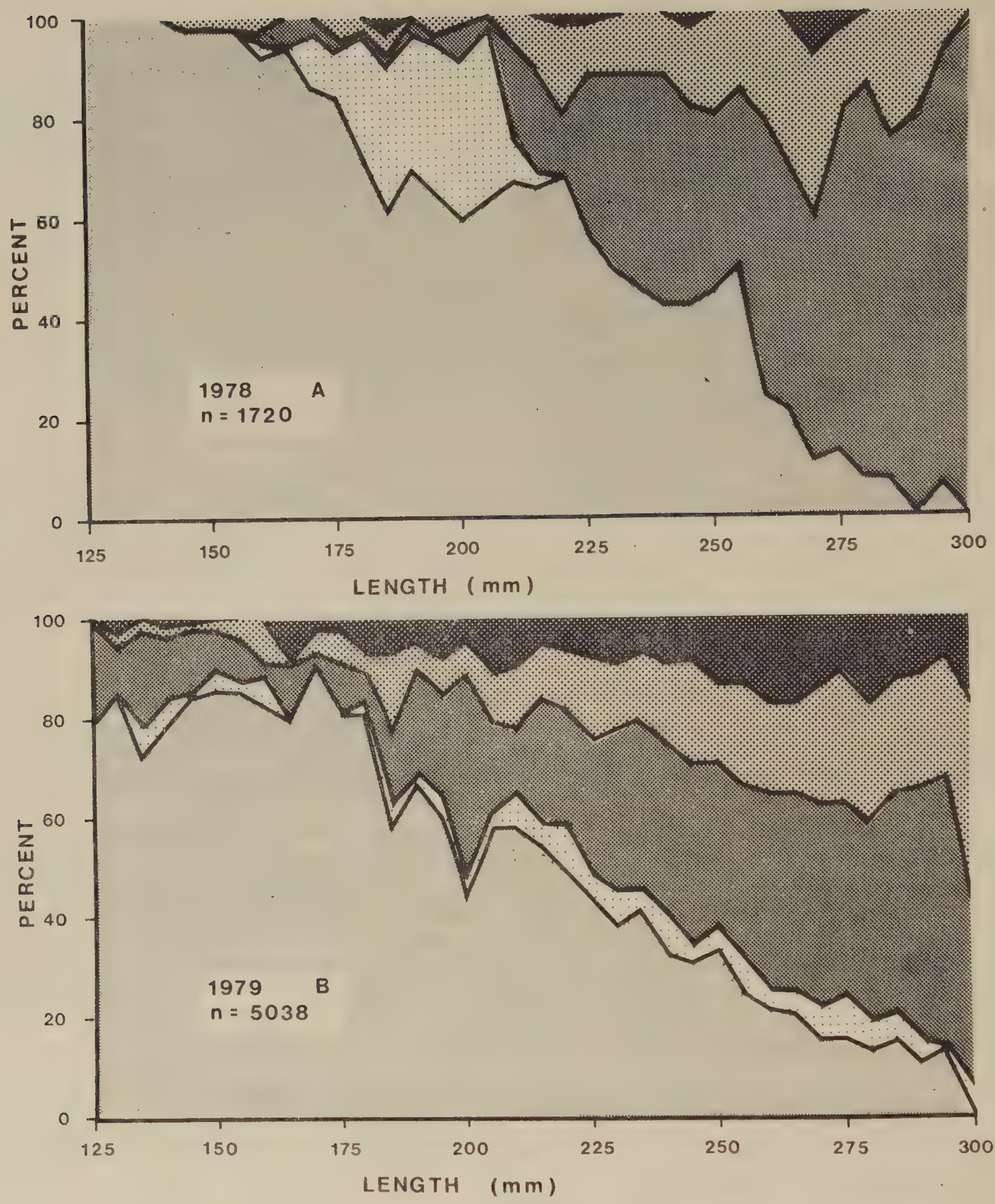
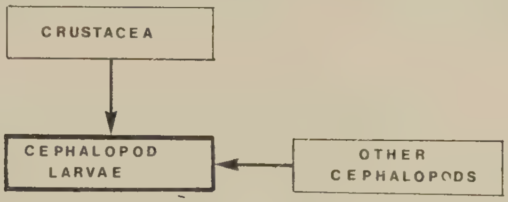


Figure 3 Percent frequency of occurrence of three main prey types found in *I. illecebrosus* gut, plotted against mantle length

(Durward *et al.*, 1980), but their reproductive strategy is probably based on numbers. Their rapid development in relatively warm waters also offers only a short vulnerable period during their egg stage. On the other hand, the shallow-water benthic egg masses are often provided with a protective firm gelatinous encasement or capsule (sepioides and myopsids). In the case of octopods, females brood their egg masses, and hence survival opportunities are maximized.

In the larval or post-embryonic stage distributions, two ecosystems were identified: the planktonic and the benthic. In their feeding patterns, however, a single model was apparently applicable to both forms of livelihood. The model will describe them as "predators of crustacea". (This model is applicable to all cephalopods studied and hence will be referred to as the "standard model" for convenience.) All hatchlings are active predators as soon as their predatory equipment is developed. While most hatchlings begin capturing prey soon after hatching, ommastrephids go through the Rhynchoteuthion stage before predation begins. The prey type was consistently crustacean, in both larval and adult forms.

Another less important component to cephalopod larval predation is cannibalism. Cannibalism, however, was not applicable to some of the young examined, but warranted representation in our model. The model may be represented as follows.



In order to consider predators of caphalopod young, it is necessary to separate planktonic from benthic forms. In general, the planktonic cephalopod hatchlings, e.g., *Loligo* (Fields, 1965), *Illex* (Amaratunga, Rowell and Roberge, 1980) *Todarodes* (Hamabe, 1962) are commonly associated with productive areas of water masses, e.g., upwellings and warm current interphases (Amaratunga, Rowell and Roberge, 1980; Hamabe, 1962). In these areas it is likely that cephalopods fall prey to the various predators in the plankton assemblages ranging from ctenophores, arrow worms and siphonophores (listed for *L. opalescens*; Fields, 1965) to larger forms, such as fish and even whales (while they are feeding on krill) at the highest trophic levels.

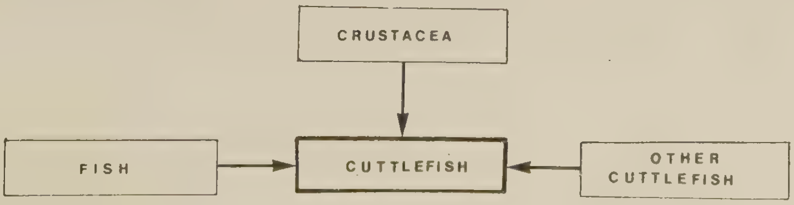
The benthic hatchlings, on the other hand, quickly develop defence and camouflage tactics. These specializations thus require specialized predators as well. If one is to generalize, it could be envisaged that these agile and attentive young will fall prey to only the more active predators such as demersal fish.

3.2 Juvenile and Adult Stages

Finally, let us consider the juvenile and adult forms. Here, each cephalopod group will be considered separately.

3.2.1 Sepioidea

Cuttlefish predatory activities are well defined. They visually control their nocturnal feeding habits and thus have a well-developed capacity to select prey. The selected prey are primarily crustaceans such as prawn and crab. These are usually detritus feeders or scavengers. Cuttlefish will also feed (less often) on fish and smaller cuttlefish. Again, the standard prey preference model fits this group and may be represented as follows:

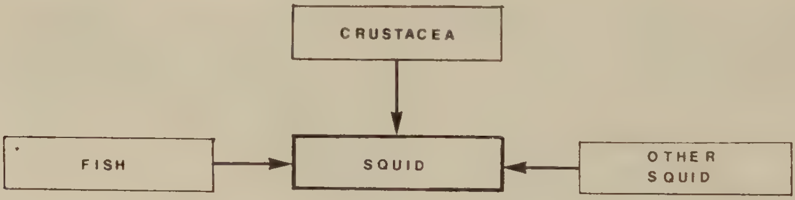


There are in fact no major differences between the feeding model of the early young and the juveniles ranging to adult ages. There are, however, obvious size preferences related to growth of cuttlefish.

In their benthic habitats, these cephalopods are known to deploy predator evasion tactics by sometimes burying themselves, and at other times by camouflage colour displays. Thus, their most vulnerable period is during nocturnal excursions from their hiding places. Limited information is available on the predators or cuttlefish. The primary predators are demersal fish, but others may be important. Nevertheless, cuttlefish in the trophic chain would represent energy transference mainly from the detritus feeder to the upper trophic levels.

3.2.2 Teuthoidea

Feeding patterns adopted by both myopsid and oegopsid juvenile and adult stages are by and large similar (Vovk, 1974; Amaratunga, 1980). Both groups contain perpetual swimmers leading an active predatory mode of life. Schooling is typical (Amaratunga, 1980); and hence gregarious predatory activity is prevalent. The most important prey component is crustacean, and once again our standard prey preference model may be applied. There are also important fish and squid components, and the model may be represented as follows:



This model has a number of qualifiers, primarily related to the areal and age variations.

(i) In all instances, crustaceans form the most important component in the juvenile stages. An exception perhaps is among the largest (sexually maturing and mature) oegopsids when cannibalism predominates (Amaratunga, 1980).

(ii) Importance of fish and other squid (cannibalism) increases with age (size) of the predator.

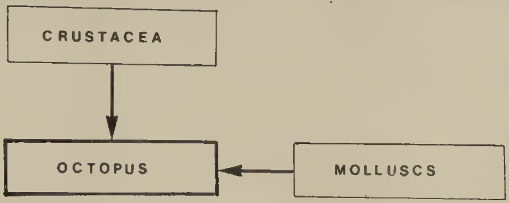
(iii) Because of the extreme mobility of squid, each prey component may constitute many species. This was especially apparent in the myopsids, where minor prey types such as gastropods, polychaetes, etc. were noted (Fields, 1965; Karpov and Cailliet, 1978; Vovk, 1974).

In summary, teuthoids are by far the largest contributors to the cephalopod biomass and energy transfer from the ecosystem to this biomass is primarily from planktonic (and occasionally nektonic) crustacea, and to a lesser degree from nektonic fish and squid smaller in size than the predator. It should also be noted that in the case of cannibalism (or predation on other squid) we are in actual fact seeing an intermediate step in energy transfer between the (mainly) crustacean prey and the final predators on squid.

Predators on teuthoids are numerous and diverse; both demersal and pelagic (see Table 2 of Appendix prepared for *L. pealei* and *I. illecebrosus* by Lange, 1980) including fish, sea birds and marine mammals. There are also cases where the predator and prey reverse roles, as well as compete with one another in the ecosystem. Such interrelationships were described for *L. pealei*, herring and silver hake (Vovk, 1974). Numerous records of sea bird predation are known (Ennis and Collins, 1979; Rechsiek and Frey, 1978). Marine mammals are heavy predators and here toothed whales are by far the most important; e.g., many estimations of squid consumption by whales demonstrate pilot whales (Mercer, 1973), sperm whales (Clarke, 1977; Kawakami, 1980).

3.2.3 Octopus

The octopus is a bottom dweller, and mostly preys on benthic forms. The prey types are predominantly crustacea (mainly crab) and molluscan gastropods and bivalves. This again fits the standard prey preference model which may be represented as follows:



As in cuttlefish, prey preference does not alter very much with age, although size-related changes obviously occur.

Predation on octopus is again not well documented. The largest predators are probably the demersal fish which will prey only on the manageable sizes of octopus, but it is difficult to envisage heavy predation on larger octopus. In the case of *O. vulgaris* in the Mediterranean areas, arms are often bitten off by eels; and it is rare that one could find a complete octopus (O'Dor, pers. comm.). It is therefore probable that this cephalopod may attain the upper levels of the food web.

Summary

The cephalopod predation model is relatively simple and quite standard for the group. Crustacea are undoubtedly the most frequently chosen prey. The commonly identified crustacean prey types range from filter feeders eating plankton or detritus to carnivores or scavengers. Raptorial feeding and cannibalism is developed in some of the larger crustacea (Barnes, 1974). The interrelationship of prey (crustacea) and predator may be considerably simplified in the following two cases:

(a) Where the crustacean prey is a detritus feeder, cephalopods form a component of the detritus food chain (Barnes and Mann, 1980), i.e., detritus → detritus feeder → carnivorous cephalopod.

(b) Where the crustacean is a filter feeder, feeding on phytoplankton, it will be comprised of the grazing food chain (Barnes and Mann, 1980), i.e., plant → herbivores → carnivorous cephalopod.

In the trophic interactions it is generally accepted that the small size of the crustacean consumer usually reflects high productivity, but the proportion of energy passing up the food chain varies with generally complex factors (Barnes and Mann, 1980). For our purposes, therefore, let it suffice if we consider energy transfer from the crustacean to the cephalopod.

At the early young stages, we have observed exceedingly high feeding rates, rapid growth rates and high transfer efficiencies (Choe, 1966; Boletzky, 1974; Hurley, 1976). Choe (1966) particularly demonstrated food conversion efficiencies ranging from 11 to 56 percent in hatchlings and 29-57 percent in older cuttlefish. The average corresponded to 2.59 kg of food producing 1 kg of *Sepia* biomass. In octopus the conversion efficiency was 50 percent (Wells, 1978). Again, in young adult *Illex* it was 40 percent (O'Dor *et al.*, 1980) as compared to 56 percent at 10°C and 55 percent at 15°C for *Octopus vulgaris* (Mangold-Wirz and Boletzky, 1973).

These are all indeed very high rates as compared to fish (Choe, 1966). We may, therefore, conlcude that cephalopods are extremely effective predators, preying primarily on organisms at the first or second trophic levels. The consumed food is efficiently converted to a large biomass in the marine environment. This biomass is usually available to the higher predators, particularly to fish and whales.

4. TOWARD MORE REALISTIC MODELLING

The processes in the ecosystem are complex and it is quite difficult to understand the mechanisms that sustain any community or food web. In order to understand the processes, one must determine how numbers in a population are generated and regulated, how competition and predator/prey relationships are maintained, how energy is carried through the food chains in the ecosystem, etc. In our attempts we will consider numbers and energy transfer with special reference to the extensively studied species *Illex illecebrosus* of the northwest Atlantic.

Unlike the terrestrial environment, where the predominant organic materials being transferred through the food web are carbohydrates, in the ocean the predominant material is protein. Unlike carbohydrate energetics, where energy is stored in large amounts and retained for subsequent growth, in protein energetics, energy is used for rapid growth; like growth in individual size of organism or speed of replacement of generations. In the marine ecosystem, cephalopods grow relatively rapidly in terms of size and replacement (e.g., for *I. illecebrosus* during the most rapidly growing period, estimates as high as 1.5 mm/day have been recorded, and generations are replaced annually). However, in order to understand the ecological role of the cephalopod it is necessary to know the rate at which new material is being produced. A knowledge of productivity gives an understanding of the rates of transfer of energy and materials through the food chain (Mann, 1976).

Production is a function of growth rate and has been defined as the average number of individuals present multiplied by the mean weight change of an individual through a period of time (Mann, 1976):

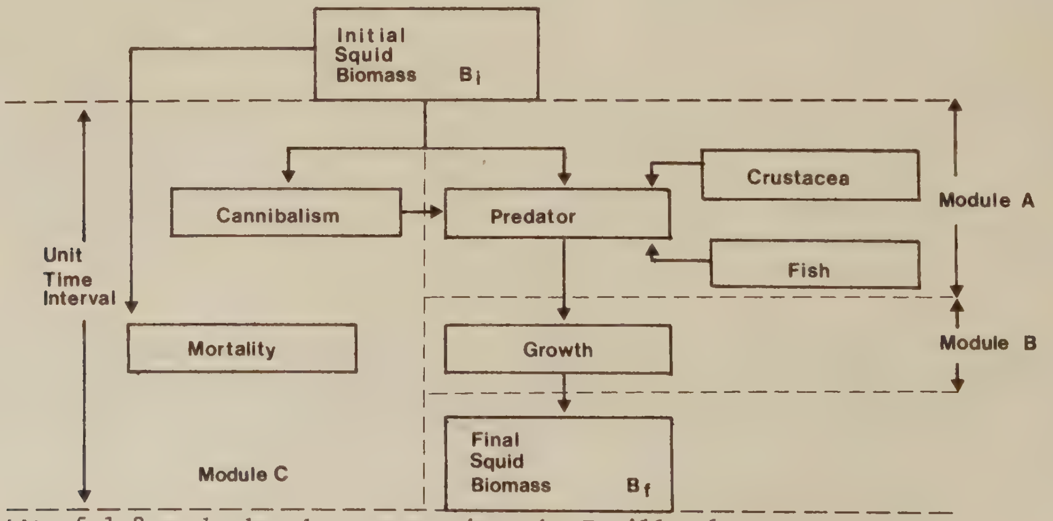
$$P = \frac{1}{2}\,(N_i + N_f)\,(W_f - W_i) \text{ ----- } (1)$$

where N_i and N_f are initial and final numbers, and W_i and W_f are initial and final weights, respectively. There is now evidence of predictability in the ratio between production and biomass, P/B, so let us first consider biomass:

Growth of an individual may be represented in terms of weight increments through the life cycle. Individual weight times the number of individuals in the population gives us the collective weight or biomass. Thus through a given time interval Δt, change in biomass is represented as:

$$\Delta B = N_fW_f - N_iW_i \text{ ----- } (2)$$

Individual weight change or growth is in turn directly related to food consumption. Thus the predation models previously described for commercial cephalopods (Section 2.4) may be included in a model which depicts changes in biomass of a population through unit time intervals of Δt:



(Δt of 1-2 weeks has been convenient in *I. illecebrosus* simulations)

Here $B_i = N_iW_i$ and $B_f = N_fW_f$. Module A represented here depicts juvenile and adult squid, but this may be replaced by any of the models described in Section 2.4 depending on the organism we wish to consider.

4.1 Module A - Predation

Models presented earlier (Section 2.4) described predation by various life history stages of cephalopods. However, quantification of these is difficult, since many studies are limited to short periods of the life stages or to instantaneous observations at a particular stage of development. Sequential observations for much of the life cycle are available for *I. illecebrosus* (Amaratunga, 1980a; Ennis and Collins, 1979). In a two-year study (Amaratunga, 1980a) quantitative data illustrated that the proportion of animals feeding in the population changing with time (Figure 2). Although between-year variations are demonstrated, fitted regressions show a general decrease in the proportion of feeding animals as the season advances, as they grow from juvenile stages to sexually maturing adults. Such decreases are likely because energy requirement per unit of body weight usually decreases with increasing body weight (O'Dor *et al.*, 1980). Recognizing that physiological demands, temperature, availability and other factors affect feeding rates, the linear functions depicted in Figure 2 provide only general estimations of feeding activity of the populations through the period that they are recruited to the fishery.

We noted earlier that most cephalopods show diurnal periodicity in feeding, with one major feeding period per day (a feeding consists of one large prey or a number of small prey). This was particularly apparent in *I. illecebrosus* (Figure 1). This phenomenon was further sustantiated by the generally quoted fast digestion rates in other species (Table 4).

Table 4

Rates of digestion quoted for adult cephalopods

Cephalopod	Rate of digestion (h)	Temperature (°C)	Author(s)
Sepia	15-20	varying	Bidder 1966
	12	varying	Gariaeff 1916
Loligo	4-6	varying	Bidder 1959, 1966
	6.6	18	Karpov and Caillet 1978
Illex	12-13	10	Wallace, O'Dor and Amaratunga 1980
	10-12	10	Boucher-Rodoni 1975
Octopus	12	30	Boucher-Rodoni 1973
	15	20	Boucher-Rodoni
	30		Boucher-Rodoni
	15-20	varying	Bidder 1966

In *I. illecebrosus* digestion rates varied with meal size, with the frequencies of smaller sustained feedings estimated at 8-12 h and larger meals taking more than 24 h (Wallace, O'Dor and Amaratunga, 1980; Boucher-Rodoni, 1975). In the laboratory when large meals were consumed, squid tended to skip the next day's diurnal feeding schedule (O'Dor *et al.*, 1980). Meal sizes ranged from traces up to 25 percent of the body weight. However, their digestive capacity limited food intake, which in the laboratory were thought not to exceed a daily 10-15 percent of the body weight. For our purposes we may quantify the sustained daily feeding rate of the population (at 10°C) at 10 percent of the average body weight.

Daily feeding rate (DFR), as defined by O'Dor *et al.* (1980), may be calculated for the model as the percentage of food consumed relative to the mean body weight of squid for each time interval (Δt) from the equation:

$$\mathrm{DFR}(\%) = \frac{F}{(W_f+W_i)/2} \cdot \frac{100}{t} \quad\text{-----}\quad (3)$$

Seasonal variations in prey preference (Figure 3) may now be interpreted in terms of DFR, to determine the impact of squid on prey in the ecosystem. Table 5 summarizes a simulation of prey biomass consumed weekly by 1 000 g of *I. illecebrosus,* assuming that the proportion of the population feeding corresponds to the linear functions (Figure 2) and that the sustained DFR of the population is 10 percent of individual body weight.

Biomass estimations for the *I. illecebrosus* stocks in 1978 and 1979 are questionable, however, the sum total of weekly landings in each year was 25 533 t and 34 882 t, respectively (Roberge and Amaratunga, 1980). The simulated impact of these biomasses on the prey are as follows:

1978: 174.4 t fish, 639.4 t crustacea, 398.2 t squid by cannibalism, and 14.7 t others (total 1 226.7 t)

1979: 214.0 t fish, 480.9 t crustacea, 339.5 t squid by cannibalism, and 20.8 t others (total 1 055.2 t)

In these simulations, biomass removed by cannibalism are represented as squid predation on an external food source, rather than an intrinsic component of the squid biomass.

4.2 Module B - Growth

It is common practice to represent growth of squid in terms of mantle length increments, and of octopus in terms of body weight increments. The von Bertalanffy curve particularly has been effectively used to describe squid growth. Applying the equation

$$L_t = L_\infty \left[1-e^{-k(to)}\right] \text{ ------ } (4)$$

where L_t is the mantle length at age t, L_∞ is the asymptotic length, and k is the growth constant, separately to three years of length data, Amaratunga (1980) described the growth cycle of *I. illecebrosus*. Mantle length was a convenient measure in this instance and provided a good fit to data sets with relatively little variations around the mean. Indeed length data of other squid and *Sepia* may be used similarly. However, growth in weight estimates are necessary to relate to feeding. The von Bertalanffy curve $W_t = W_\infty[1-e^{-k(t - t_o)}]^b$, where W is the weight of the cephalopod, is applicable here. Since weight measurements usually have considerable variation around the mean, it may be more convenient to convert data from length to weight using a relationship of the form:

$$W = aL^b$$

For *I. illecebrosus* the constants $\underline{a}$ and $\underline{b}$ have been evaluated to be of the order of 10^{-3} and 3.15, respectively.

An alternative model derived for experimental animals (Choe, 1966) uses the equation

$$DGR\ (\%) = \frac{W_f - W_i}{(W_f + W_i)/2}\ 100/t \text{ ---- } (5)$$

DGR is the daily growth rate expressed as a percentage of the change in body weight from W_i to W_f over a period of t days. Experimental conditions permit periodical weighing of individual animals, although metabolic and behavioural patterns are likely to be altered from natural conditions. Either or both methods now permits us to compare DGR and DFR (from equation 3).

An empirical relationship between growth rates and feeding rates is given by Jones (1976) as:

$$\Delta G = \alpha_2\ (\Delta F - \alpha_1) \text{ ---- } (6)$$

where ΔG = DGR and ΔF = DFR (from Module A). α_1 is food requirement when growth is zero and is referred to as the maintenance ration, and $\alpha 2$ is equivalent to the net efficiency of conversion of food into growth. By expressing growth and food intake in units proportional to the body weight, many experimental relationships between growth rate and feeding rate determined for fish, such as cod and haddock, have suggested linear relationships over their normal range of feeding rates. In these regressions, the intercept of the abscissa represents α_1 (maintenance ration) and the slope represents $\alpha 2$ (efficiency of conversion). A similar relationship is depicted in Figure 4 from experiments by O'Dor *et al.* (1980) and Hirtle (1981). Although individual variation masked some of the relationships, the estimated maintenance ration (DFRM) for squid between 150 and 250 g was 1.1 percent of their body weight, although it is recognized that maintenance energy varies in relation to physiological requirements and that there is no one maintenance level of

Table 5a

Simulation of biomass consumed by 1 000 g population of *I. illecebrosus*
(Scotian shelf ambient temperature 8-12°C)
1978

	Week No	Mean Weight of squid (g)	Weight of prey consumed (g) fish	crustacean	squid	other
June	26	126.6	3.19	43.12	6.92	-
July	27	137.9	4.72	46.11	1.57	
	28	134.8	4.64	45.38	1.55	
	29	138.4	5.58	32.98	14.71	
	30	189.6	5.49	22.46	21.96	
	31	159.9	4.42	34.35	10.30	
Aug	32	171.1	5.31	21.71	21.22	
	33	179.8	5.21	21.33	20.86	
	34	189.8	11.64	25.14	8.85	0.93
	35	199.3	7.32	21.95	15.09	1.37
Sept	36	209.4	7.18	21.55	14.82	1.35
	37	219.3	9.70	17.63	14.54	2.20
	38	229.2	9.51	17.29	14.27	2.16
	39	239.1	8.90	16.11	16.11	1.27
Oct	40	248.8	8.73	15.80	15.80	1.25
	41	258.7	8.96	16.29	13.44	2.04
	42	268.7	8.38	15.16	15.16	1.20
	43	309.0	8.60	17.19	12.50	0.39
	44	312.3	9.94	11.85	16.44	
Nov	45	314.5	7.11	13.47	16.08	0.37
	46	277.5	8.05	16.09	11.70	0.37
	47	292.2	7.51	13.58	13.58	1.07
	48	291.6	7.33	13.26	13.26	1.05
		Total	167.42	519.80	310.73	17.02

Table 5b

Simulation of biomass consumed by 1 000 g population of *I. illecebrosus*
(Scotian shelf ambient temperature 8-12°C)
1979

	Week No	Mean Weight of squid (g)	Weight of prey consumed (g) fish	crustacean	cannib	other
July	27	137.1	2.46	21.54	6.77	
	28	133.9	2.76	21.50	6.45	
	29	138.0	3.37	13.80	13.49	
	30	149.9	5.20	15.92	7.96	
	31	159.7	7.64	16.50	5.81	0.61
Aug	32	169.6	7.63	16.47	5.80	0.61
	33	179.5	6.70	14.62	9.44	0.30
	34	189.4	6.38	11.55	11.55	0.91
	35	199.3	4.86	14.57	10.01	0.91
Sept	36	209.1	4.85	14.54	10.00	0.91
	37	219.0	6.65	12.10	9.98	1.51
	38	228.9	6.64	14.49	9.36	0.30
	39	238.8	6.33	11.45	11.45	0.90
	40	248.7	6.32	11.43	11.43	0.90
Oct	41	258.5	6.61	12.01	9.91	1.50
	42	268.4	6.59	13.19	9.59	0.30
	43	308.1	5.68	10.77	12.87	0.30
	44	311.4	7.77	9.26	12.84	
Nov	45	313.7	7.74	9.24	12.82	
	46	275.5	5.65	10.71	12.80	0.30
	47	291.8	5.64	10.70	12.77	0.30
		Total	123.48	286.36	213.10	10.56

requirement for an organism. While active animals require more metabolic energy, maintenance requirements decreased with increased size of organisms. Typically, however, the basic daily requirement is proportional to body weight raised to the power 0.7-0.8 (O'Dor *et al*, 1980).

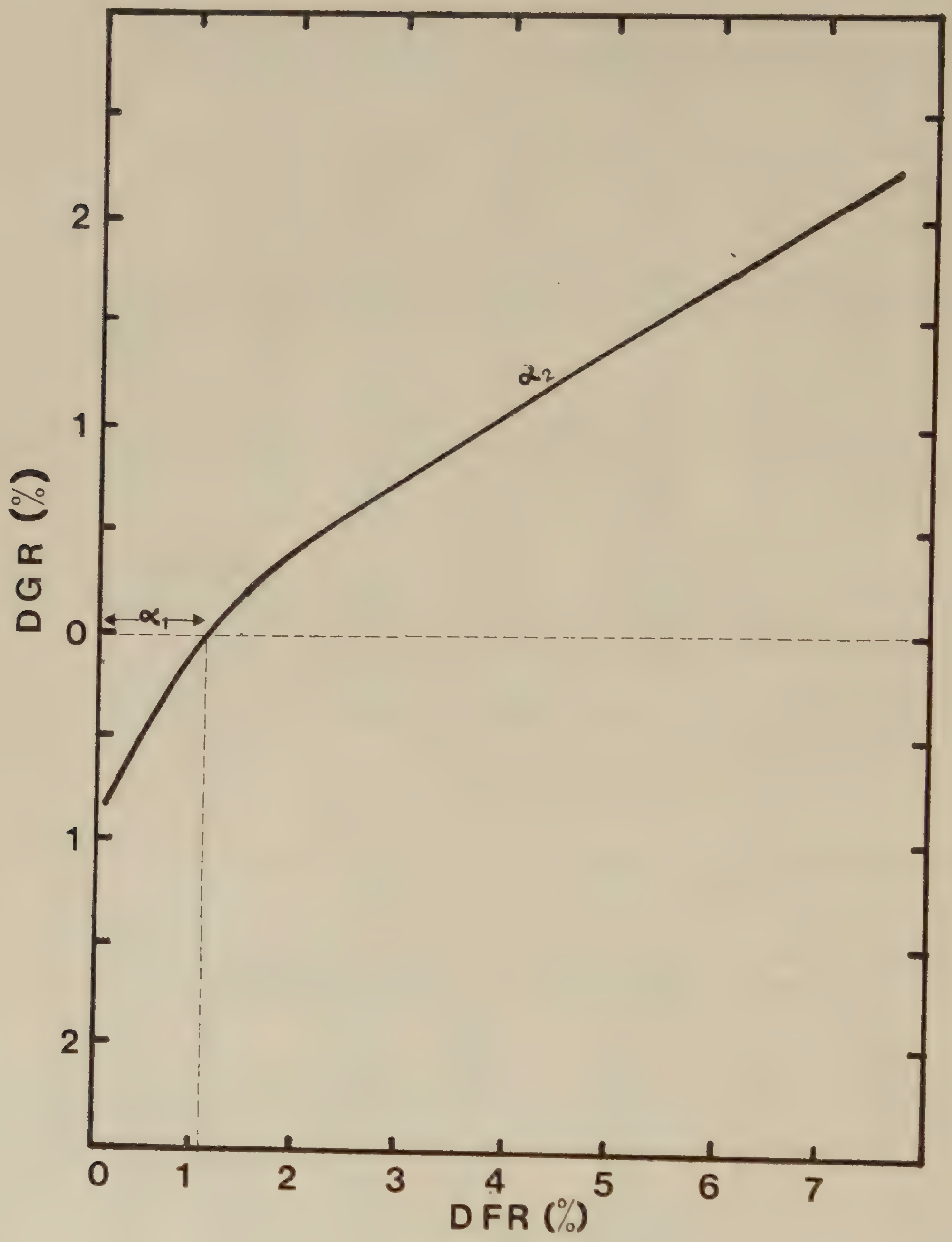


Figure 4 Mean daily growth rate (DGR) plotted against mean daily feeding rate (DFR) for laboratory-observed *Illex illecebrosus* (O'Dor *et al.*, 1980 and Hirtle, 1981); α_1 = intercept, α_2 = slope.

Not all food consumed by an organism is available for growth. Thus net conversion efficiency is described as the total quantity of food absorbed minus the food required for maintenance. The conversion efficiency (calculated from the two segments of the curves in Figure 4) for the laboratory population ranged from 33 to 51 percent (O'Dor *et al.*, 1980). Winberge (1956) using a generalized value, suggested 80 percent of the total food was effectively available. Thus the growth rate model (equation 6) was generalized as:

$$DGR = 0.8\ DFR - DGRM \text{ ----- } (7)$$

Although Wallace, O'Dor and Amaratunga (1981) estimated efficiency of conversion for *I. illecebrosus* at 86 percent, and it is generally accepted that efficiency is high, a satisfactory model for cephalopods in general should have an efficiency in the range of 50-70 percent (71 percent was observed in young *Sepia)*.

4.3 Module C - Numbers

Our basic population model (equation 2) represents the change in biomass of a population through time. We have considered the estimation of weight change through unit intervals of time and now we must estimate changes in numbers through the same intervals. Modifications of the cohort analysis are among the models proposed for *I. illecebrosus* (Hurley and Waldron, 1978). Here estimates were made of mortality rates and initial population size by back calculating from the decrease in numbers through the period squid are exploited in the fishery. Caddy (1979) identified that changes in numbers during the exploited phase should incorporate immigration (when young squid migrate into the fishing grounds) and emigration (when mature adults leave the fishing grounds to spawn) as factors of mortality. However, it is difficult to determine immigration rates (or times), and it is more reasonable to assume that the population is closed at the time of recruitment of the stock to the fishery. For *I. illecebrosus* stocks on the Scotian shelf, this assumption is reasonable because immigration to the fishing grounds begin as early as May and the fishery opens on 1 July each year. Mohn (1982) interpreted that the total mortality factor (Z) will then consist of: fishing mortality (F), mortality due to cannibalism (MC), mortality through emigration (ME) and all other conventional natural mortalities (MN).

The basic equation for the fate of the number of individuals (N) is given as:

$$\frac{dN}{dt} = -ZN \text{ ----- } (8)$$

Since $Z = F+MC+ME+MN$, in each time interval (dt), the number of survivors (N_f) from an initial number (N_i) will be:

$$N_f = N_i\ e^{-(F+MC+ME+MN)\ dt} \text{ ----- } (9)$$

Mohn's simulation defines fishing mortality; $F = qf$ is as the product of catchability coefficient and standardized fishing effort. Effort patterns for the *I. illecebrosus* fishery on the Scotian shelf were given for 1978 and 1979 by Amaratunga (pers. comm.), and mesh selection studies (Amaratunga, Kawahara and Kono, 1979) provide input values to q.

Cannibalism: Mohn (1982) described mortality due to cannibalism mathematically as follows: If 1 unit of animals entered a feeding period (e.g., 1-2 weeks) and Y of them were alive at the end of the period and HY were eaten by their cohorts, then:

$$1 = Y + HY \text{ ----- } (10)$$

H which varies as the animal grows, was discussed earlier (Module A). In each time interval there will be a number of feeding periods (NFP), which was also estimated earlier (Module A). the mortality due to cannibalism for each time interval is then given as:

$$MC = NFP\ \ln\ (1 + H) \text{ ----- } (11)$$

Emigration: Here emigration is treated as mortality. Data for 1978 and 1979 from Amaratunga (1980) shows that onset of late maturity stages in *I. illecebrosus* initiates their spawning migration. Maturity ogives show the proportions reaching these maturity stages in relation to the season.

Natural mortality: Mohn (1982) following the arguments of many authors chose a constant exponential rate to be 0.6/period.

Since cephalopods are shortlived and often one generation totally replaces another, traditional fisheries models are not ideally suited for our purposes. Yet we see many of the biological parameters required for the basic biomass model (equation 2) are quantifiable, particularly for *I. illecebrosus*. Indeed many attempts have been made to simulate *I. illecebrosus* stocks. With each attempt we gain further insight and draw closer to more realistic modelling. Knowledge of the biomass change and production is the basis for our understanding of the role of cephalopods in the ecosystem; how production of new tissue is effected by reproduction and by feeding regimes, and how these numbers are balanced by losses due to mortality factors.

5. REFERENCES

Amaratunga, T., 1980 Growth and maturation patterns of short-finned squid, *Illex illecebrosus*, on the Scotian Shelf. NAFO SCR Do. 80/KK/30, Ser. No. N062:17 p.

____________, 1980a Preliminary estimates of predation by short-finned squid, *Illex illecebrosus*, on the Scotian Shelf. NAFO SCR Doc. 80/II/31, Ser. No. N063

Amaratunga, T. and F. Budden, 1981 Abundance estimates of *Illex illecebrosus*.NAFO SCR Doc. 81/IX/100, Ser. No. N366

Amaratunga, T., A. Kawahara, and H. Kono, 1979 Mesh selection of the short-finned squid *Illex illecebrosus* on the Scotian Shelf, using a bottom trawl: a joint Canada-Japan 1978 research program ICNAF Res. Doc. 79/II/35

Amaratunga, T., T.W. Rowell and M. Roberge, 1980 Summary of joint Canada/USSR research program on the short-finned squid, *Illex illecebrosus*, February 16 to June 4, 1979. NAFO SCR Doc. 80/II/38, Ser. No. N069

Barnes, R.K., 1974 Invertebrate zoology. Toronto, Saunders Co., 786 p.

Barnes, R.K. and K.H. Mann, 1980 Fundamentals of aquatic ecosystems. Osford, Blackwell Scientific Publications, 229 p.

Bidder, A.M., 1950 The digestive mechanism of European squids, *Loligo vulgaris*, *Loligo forbesi*, *Alloteuthis media* and *Alloteuthis subulata*. Q.J.Microsc.Sci., 91(1):1-43

____________, 1966 Feeding and digestion in cephalopods. In Physiology of the mollusca, edited by K.M. Wilber and C.M. Yonge New York, Academic Press, vol. 2:97-124

Bigelow, H.B. and M. Leslie, 1930 Reconnaissance of the waters and plankton of Monterey Bay, July 1928. Bull.Mus.Comp.Zool.Harvard Coll. 70(5):427-581

Boletzky, S.V., 1974 The "larvae" of Cephalopoda - a review. Thalassia Jugosl., 10:45-76

____________, 1977 Post-hatching behaviour and mode of life of cephalopods. Symp.Zool.Soc. Lond., 38:557-67

Boletzky, S.V. *et al.*, 1971 Laboratory rearing of Sepiolinae (Mollusca: Cephalopoda) Mar. Biol., 8:82-7

Boletzky, S.V., L. Rowe and L. Aroles, 1973 Spawning and development of the eggs, in the laboratory of, *Illex coindetti*. Veliger, 15:257-8

Boucher-Rodoni, R., 1973 Vitesse de digestion d'*Octopus cyanea* (Cephalopoda, Octopoda) Mar. Biol., 18:237-42

____________, 1975 Vitesse de digestion chez les cephalopodes *Eledone cirrosa* (Lamarck) et *Illex illecebrosus* (LeSueur). Cah.Biol.Mar., 16:159-75

Bradbury, B.E. and F.A. Aldrich, 1969 Observations on the locomotive of the short-finned squid, *Illex illecebrosus*. Can.J.Zool., 47:741-44

Caddy, J.F., Preliminary analysis of mortality, immigration and emigration of *Illex*
1979 populations on the Scotian Shelf. ICNAF Res. Doc. 79/VI/120, Ser. No. 5488

Choe, S., On the growth, feeding rates and the efficiency of food conversion for cuttle-
1966 fishes and squids. Korean J.Zool., 10(2):12-20

____________, On the eggs, rearing, habits of the fry and growth of some Cephalopoda.
1966a Bull.Mar.Sci., 16:330-48

Chun, C., *Rhynchoteuthis*. Eine merkwurdige Jungendform von Cephalopoden. Zool.Anz.,
1903 26:716-7

Clarke, M.R., A review of the systematics and ecology of oceanic squids. Adv.Mar.Biol.,
1966 5:19-300

____________, Beaks, nets and numbers. Symp.Zool.Soc.Lond., 38:89-126
1977

Durward, R.D., T. Amaratunga and R.K. O'Dor, Maturation index and fecundity for female
1979 squid *Illex illecebrosus* (LeSueur, 1831). ICNAF Res. Bull., (14)

Durward, R.D., *et al.*, Reproduction in squid, *Illex illecebrosus:* first observations in
1980 captivity and implications for the life cycle. ICNAF Sel.Pap., 6:7-13

Ennis, G.P. and P.W. Collins, Food and feeding of the short-finned squid, *Illex*
1979 *illecebrosus*, during its seasonal occurrence in the Newfoundland area.
ICNAF Sel. Pap., 5:25-9

Fedulov, P.P. and T. Amaratunga, On dates of short-finnedsquid, *Illex illecebrosus*,
1981 immigration onto the Scotian Shelf. NAFO SCR Doc. 81/VI/32, Ser. No. N311

Fields, W.G., The structure, development, food relations, reproduction and life history
1965 of the squid, *Loligo opalescens* Berry. Fish.Bull.Calif.Dep.Fish.Game,
(131):1-108

Fioroni, P., Die Entwicklungstypen der Mollusken, eine vergleichend - embryologiche.
1971 Studie. Z.Wiss.Zool., 182:263-394

Gariaeff, V.P., The digestive mechanism of European squid, *Loligo vulgaris*, *Loligo forbesi*,
1916 *Alloteuthis media* and *Alloteuthis subulata*. J.Micro.Sci. 91(1):1-43

Gulland, J.A., The fish resources of the ocean. West Byflect, Survey, Fishing New (Books)
1971 Ltd., for FAO 255 p. Rev. ed. of FAO Fish.Tech.Pap., (97):425 p. (1970)

Hamabe, M., Embryological studies on the common squid, *Ommastrephis sloani pacificus*
1962 Steenstrup, in the southwestern waters of the Sea of Japan. Bull.Jap.Sea
Reg.Fish.Res.Lab., 10:1-45

Hardy, A.C., The herring in relation to its animate environment. Part 1, The food and
1924 feeding habits of the herring. Fish.Invest.Minist.Agric.Fish.Food G.B.
(2 Sea Fish.), 7(3)

Hollingshead, K.W. and S. Corey, Aspects of the life history of *Meganyctiphanes norvegica*
1974 (M. Sars), crustacea (Euphausiacea), in Passamaguoddy Bay. Can.J.Zool., 56(3):
492-506

Hirtle, R.W.M., Bioenergetics of feeding and growth in the Atlantic squid, *Illex*
1981 *illecebrosus*. M.Sc. Thesis. Dalhousie University, Halifax, N.S., Canada

Hurley, A.C., Feeding behaviour, food consumption, growth, and respiration of the squid
1976 *Loligo opalescens* raised in the laboratory. Fish.Bull.NOAA/NMFS, 74:176-82

Hurley, G.V. and D.E. Waldron, 1977 population estimates for squid (*Illex illecebrosus*)
1978 in ICNAF Subarea 4 from the international fishery in 1977. ICNAF Res.Doc. 78/VI/61

Itami, K., *et al.,* Notes on the laboratory culture of the octopus larvae. Bull.Jap.Soc.
1963 Sci.Fish., 29:514-20

Jones, R., Growth of fishes. In The ecology of the seas, edited by D.H. Cushing and
1976 J.J. Walsh. Oxford, Balckwell Scientific Publications, p.p. 251-79

Juanico, M., Developments in South American squid fisheries. Mar.Fish.Rev., 42(7-8):10-4
1980

Karpov, K.A. and G.M. Cailliet, Feeding dynamics of *Loligo opalescens*. Fish.Bull.169:45-65
1978

Kawakami, T., A review of sperm whale food. Sci.Rep.Whales Res.Inst., (32):199-218
1980

Kulka, D.W., The life history of *Thysanoessa inermis* (Kroyer) and the community structure
1977 of Euphausiids in the Bay of Fundy. M.Sc. Thesis, University of Guelph, Guelph, Ontario, 167 p.

Kulka, D.W. and S. Corey, The life history of *Thysanoessa inermis* (Kroyer) in the Bay of
1978 Fundy. Can.J.Zool., 56(3):492-506

Lane, F.W., The kingdom of the octopus. London, Jarrolds, 287 p.
1957

Lange, A.M.T., The biology and population dynamics of the squids, *Loligo pealei* (LeSueur)
1980 and *Illex illecebrosus* (LeSueur), from the northwest Atlantic. M.Sc. Thesis, University of Washington, 168 p.

McMahon, J.J. and W.C. Summers, Temperature effects on the developmental rate of squid.
1971 Biol.Bull.Mar.Biol.Lab.,Woods Hole, 141:561-7

Mangold-Wirz, L., Biologie des céphalopodes benthiques et nectoniques de la Mer Catalane.
1963 Vie Milieu, Suppl. 13:285 p.

Mangold-Wirz, K. and S.V., Boletzky, New data on reproductive biology and growth of
1973 *Octopus vulgaris* Mar.Biol., 19:7-12

Mann, K.H., Production on the bottom of the sea. In The ecology of the seas, edited by
1976 D.H. Cushing and J.J. Walsh. Oxford, Blackwell, Scientific Publications, p.p. 225-50

Mercer, M.C., Sexual maturity and sex ratios of the ommastrephid squid, *Illex illecebrosus*
1973 (LeSueur, 1821), at Newfoundland (Subarea 3). ICNAF Res. Doc. 75/71, Ser. No. 3023

Mercer, M.C. and G. Paulmier, Distribution and biological characteristics of the short-
1974 finned squid (*Illex illecebrosus*) on the continental shelf of Subareas 3 and 4 in May-June, 1973. ICNAF Res. Doc. 74/87, Ser. No. 3323

Messenger, J.B., The visual attack of the cuttlefish, *Sepia officinalis*. Anim.Behav.,
1968 16:342-57

__________, Prey-capture and learning in the cuttlefish, *Sepia*. Symp.Zool.Soc.Lond.,
1977 38:347-76

Mohn, R.K., Yield-per-recruit analysis of short-finned squid on the Scotian Shelf by
1982 simulation. NAFO Sci.Counc.Stud., 3:39-45

Morton, J.E. and C.M. Younge, Classification and structure of the mollusca. In Physiology
1968 of mollusca, edited by K.M. Wilber and C.M. Younge. New York, Academic Press,
vol. 1

Neil, S.R. and J.M. Cullen, Experiments on whether schooling by their prey affects the
1974 hunting behaviour of cephalopods and fish predators. J.Zool.Lond., 1972:549-69

O'Dor, R.K., *et al.*, Feeding and growth in captive squid, *Illex illecebrosus*, and the
1980 influence of food availability on growth in the natural population. ICNAF
Sel.Pap., 6:15-21

O'Dor, R.K., N. Balch and T. Amaratunga, The embryonic development of the squid, *Illex*
1981 *illecebrosus*, in the laboratory. NAFO SCR Doc., Ser. No. N308:11 p.

Okiyama, M., Some considerations on the eggs and larvae of the common squid *Todarodes*
1965 *pacificus* Steenstrup. Bull.Jap.Sea Reg.Fish.Res.Lab., (15):39-53

Okutani, T., Studies on early life history of decapodan Mollusca. 1. A synoptic report
1965 on Rhynchoteuthion larva of *Todarodes pacificus* Steenstrup. Bull.Tokai Reg.
Fish.Lab. 41:23-31 (in Japanese) English translation issued as Transl.Ser.
Fish.Res.Board Can. (1058):12 p. (1968)

___________, Stock assessment of cephalopod resources fished by Japan. FAO Fish.Tech.
1977 Tech.Pap., (173):62 p.

Okutani, T. and J.A. McGowan, Systematics, distribution, and abundance of the epiplank-
1969 tonic squid (Cephalopoda, Decapoda) larvae of the California current, April
1954-March 1957. Bull. Scripps.Inst.Oceanogr., 14:1-90

Pfeffer, G., Die Cepahlopoden. Nord.Plankton, 4:9-116
1980

Recksiek, C.W. and H.W. Frey, Biological, oceanographic, and acoustic aspects of the
1978 market squid, *Loligo opalescens* Berry. Bull.Calif.Dep.Fish Game, (169):185 p.

Roberge, M.M. and T. Amaratunga, A review of the *Illex* fishery in Subareas 3 and 4 with
1980 special reference to 1978 and 1979 FLASH data. NAFO SCR Doc. 80/II/32, Ser.
No. N064

Roper, C.F.E. and C.C. Lu, Rhynchoteuthon larvae of ommastrephid squids of the western
1979 north Atlantic, with the first description of larvae and juveniles of *Illex*
illecebrosus. Proc.Biol.Soc.Wash., 91(4):1039-59

Shojima, Y., The common squid, *Todarodes pacificus*, in the east China Sea. 2. Eggs,
1972 larvae and spawning ground. Bull.Seikai Reg.Fish.Res.Lab., (42):25-58

Squires, H.J., Squid, *Illex illecebrosus* (LeSueur), in the Newfoundland fishing area.
1957 J.Fish.Res.Board Can., 14(5):693-728

Verrill, A.E., Report on the cephalopods of the northeastern coast of America. Rep.U.S.
1882 Comm.Fish., 1879(Pr.7):211-455

Vinogradov, V.I. and S.S. Noskov, Feeding of short-finned squid, *Illex illecebrosus*,
1979 and long-finned squid, *Loligo pealei*, off N.S. and New England, 1974-1975.
Sel.Pap.ICNAF, 5:31-6

Voss, G.L., Cephalopod resources of the world. FAO Fish.Circ., (149):1-175
1973

___________, Classification of recent cephalopods. Symp.ZoolSoc.Lond., 38, appendix
1977 table

Vovk, A.N., The position of the long-finned squid, *Loligo pealei* Les., in the ecosystem.
1974 Tr.Vses.Nauchno-Issled.Inst.Morsk.Rybn.Khoz.Okeanogr., 58:168-76. English
translation issued as Transl.Ser.Fish.Mar.Serv.Can., (3977)

Wallace, I.C., R.K. O'Dor and T. Amaratunga, Sequential observations on gross digestive
1980 processes of *Illex illecebrosus*. NAFO Sci.Coung.Stud., (1):65-9.

Ward, P., *et al.*, Notes on animal weight, cameral fluids, swimming speed, and color polymorphism of cephalopod *Nautilus pompilius* in the Fiji Islands. Paleobiology,
1977 3:377-88

Wells, M.J., Factors affecting reactions to Mysis by newly hatched *Sepia*. Behaviour
1958 13:96-111

____________, Early learning in *Sepia*. Symp.Zool.Soc.Lond., 8:149-69
1962

____________, Cephalopod sense organs. In Physiology of Mollusca, edited by K.M. Wilbur
1966 and C.M. Younge. New York, Academic Press, vol. 2:523-45

____________, Octopus. Physiology and behaviour of an advanced invertebrate. London,
1978 Chapman and Hall, 417 p.

Williams, L.W., The anatomy of the common squid *Loligo pealei* (LeSueur). Leiden, E.J.
1909 Brill, 92 p.

Winberg, G.G., Rate of metabolism and food requirements of fishes. Transl.Ser.Fish.
1956 Res.Board Can., (194):202 p.

Worms, J., L'utilisation des prises commerciales en biologie des pêches. Application à
1979 l'étude d'une population de *Loligo vulgaris* (Cephalopod, Teuthiodea), du Golfe du Lion. Laboratoire l'Hydrobiologie Marine. M.Sc. Thesis

Young, J.Z., The central nervous system of *Nautilus*. Philos.Trans.R.Soc. Biol.Sci.,
1965 249:1-25

____________, Brain, behaviour and evolution. Symp.Zool.Soc.Lond., 38:377-434
1977

APPENDIX

Table 1

Classification of Recent Cephalopods[1]

- *Class* **CEPHALOPODA** Cuvier, 1798
  - *Subclass* **NAUTILOIDEA** Agassiz, 1847
    - *Family* **Nautilidae** Blainville, 1825
      - *Nautilus* Linné, 1758
  - *Subclass* **COLEOIDEA** Bather, 1888
    - *Order* **Sepioidea** Naef, 1916
      - *Family* **Spirulidae** Owen, 1836
        - *Spirula* Lamarck, 1801
      - *Family* **Sepiidae** Keferstein, 1866
        - *Sepia* Linné, 1758
        - *Sepiella* Gray, 1849
      - *Family* **Sepiadariidae** Naef, 1912
        - *Sepiadarium* Steenstrup, 1881
        - *Sepioloidea* Orbigny, 1840
      - *Family* **Sepiolidae**
        - *Subfamily* **Rossiinae** Appellöf, 1898
          - *Rossia* Owen, 1834
          - *Semirossia* Steenstrup, 1887
          - *Neorossia* Boletzky, 1971
        - *Subfamily* **Heteroteuthinae**
          - *Heteroteuthis* Gray, 1849
          - *Nectoteuthis* Verrill, 1883
          - *Iridoteuthis* Naef, 1912
          - *Stoloteuthis* Verrill, 1881
          - *Sepiolina* Naef, 1912
        - *Subfamily* **Sepiolinae** Appellöf, 1898
          - *Sepiola* Leach, 1817
          - *Euprymna* Steenstrup, 1887
          - *Rondeletiola* Naef, 1921
          - *Sepietta* Naef, 1912
          - *Inioteuthis* Verrill, 1881
      - *Family* **Idiosepiidae** Appellöf, 1898
        - *Idiosepius* Steenstrup, 1881
    - *Order* **Teuthoidea** Naef, 1916
      - *Suborder* **Myopsida** Orbigny, 1845
        - *Family* **Pickfordiateuthidae** Voss, 1953
          - *Pickfordiateuthis* Voss, 1953
        - *Family* **Loliginidae** Steenstrup, 1861
          - *Loligo* Schneider, 1784
          - *Doryteuthis* Naef, 1912
          - *Lolliguncula* Steenstrup, 1881
          - *Sepioteuthis* Blainville, 1824
          - *Alloteuthis* Wülker, 1920
          - *Uroteuthis* Rehder, 1945
          - *Loliolus* Steenstrup, 1856
          - *Loliolopsis* Berry, 1929
      - *Suborder* **Oegopsida** Orbigny, 1845
        - *Family* **Lycoteuthidae** Pfeffer, 1908
          - *Subfamily* **Lycoteuthinae** Pfeffer, 1908
            - *Lycoteuthis* Pfeffer, 1908
            - *Selenoteuthis* Voss, 1958
            - *Nematolampas* Berry, 1913
          - *Subfamily* **Lampadioteuthinae** Berry, 1916
            - *Lampadioteuthis* Berry, 1916
        - *Family* **Enoploteuthidae** Pfeffer, 1900
          - *Subfamily* **Enoploteuthinae** Pfeffer, 1912
            - *Enoploteuthis* Orbigny, 1839
            - *Abralia* Gray, 1849
            - *Abraliopsis* Joubin, 1896
            - *Watasenia* Ishikawa, 1913
          - *Subfamily* **Ancistrocheirinae** Pfeffer, 1912
            - *Ancistrocheirus* Gray, 1849
            - *Thelidioteuthis* Pfeffer, 1900
          - *Subfamily* **Pyroteuthinae** Pfeffer, 1912
            - *Pyroteuthis* Hoyle, 1904
            - *Pterygioteuthis* Fischer, 1896
        - *Family* **Octopoteuthidae** Berry, 1912
          - *Octopoteuthis* Rüppell, 1844
          - *Taningia* Joubin, 1931
        - *Family* **Onychoteuthidae** Gray, 1849
          - *Onychoteuthis* Lichtenstein, 1818
          - *Onykia* Lesueur, 1821
          - *Chaunoteuthis* Appellöf, 1890
          - *Ancistroteuthis* Gray, 1849
          - *Moroteuthis* Verrill, 1881
          - *Kondakovia* Filippova, 1972
        - *Family* **Cycloteuthidae** Naef, 1923
          - *Cycloteuthis* Joubin, 1919
          - *Discoteuthis* Young & Roper, 1969
        - *Family* **Gonatidae** Hoyle, 1886
          - *Gonatus* Gray, 1849
          - *Gonatopsis* Sasaki, 1920
          - *Berryteuthis* Naef, 1921
        - *Family* **Psychroteuthidae** Thiele, 1921
          - *Psychroteuthis* Thiele, 1921
        - *Family* **Lepidoteuthidae** Naef, 1912
          - *Lepidoteuthis* Joubin, 1895
          - *Pholidoteuthis* Adam, 1950
          - *Tetronychoteuthis* Pfeffer, 1900
        - *Family* **Architeuthidae** Pfeffer, 1900
          - *Architeuthis* Steenstrup, 1857
        - *Family* **Histioteuthidae** Verrill, 1881
          - *Histioteuthis* Orbigny, 1841
        - *Family* **Neoteuthidae** Naef, 1921
          - *Alluroteuthis* Odhner, 1923
          - *Neoteuthis* Naef, 1921
        - *Family* **Bathyteuthidae** Pfeffer, 1900
          - *Bathyteuthis* Hoyle, 1885
        - *Family* **Ctenopterygidae** Grimpe, 1922
          - *Ctenopteryx* Appellöf, 1899
        - *Family* **Brachioteuthidae** Pfeffer, 1908
          - *Brachioteuthis* Verrill, 1881
        - *Family* **Batoteuthidae** Young & Roper, 1968
          - *Batoteuthis* Young & Roper, 1968
        - *Family* **Ommastrephidae** Steenstrup, 1857
          - *Subfamily* **Illicinae**
            - *Illex* Steenstrup, 1880
            - *Todaropsis* Girard, 1890
          - *Subfamily* **Todarodinae**
            - *Todarodes* Steenstrup, 1880
            - *Nototodarus* Pfeffer, 1912
            - *Martialia* Rochebrune & Mabille, 1889
            - *Ornithoteuthis* Okada, 1927
          - *Subfamily* **Ommastrephinae**
            - *Ommastrephes* Orbigny, 1835
            - *Dosidicus* Steenstrup, 1857
            - *Symplectoteuthis* Pfeffer, 1900
            - *Hyaloteuthis* Gray, 1849
        - *Family* **Thysanoteuthidae** Keferstein, 1866
          - *Thysanoteuthis* Troschel, 1857
          - *Cirrobrachium* Hoyle, 1904
        - *Family* **Chiroteuthidae** Gray, 1849
          - *Chiroteuthis* Orbigny, 1839
          - *Valbyteuthis* Joubin, 1931
        - *Family* **Mastigoteuthidae** Verrill, 1881
          - *Mastigoteuthis* Verrill, 1881
        - *Family* **Promachoteuthidae** Naef, 1912
          - *Promachoteuthis* Hoyle, 1885
        - *Family* **Grimalditeuthidae** Pfeffer, 1900
          - *Grimalditeuthis* Joubin, 1898
        - *Family* **Joubiniteuthidae** Naef, 1922
          - *Joubiniteuthis* Berry, 1920

---

[1] Reproduced from Roper, Sweeney and Nauer, 1983

Table 1 (continued)

- *Family* **Cranchiidae** Prosch, 1849
  - *Subfamily* **Cranchiinae** Prosch, 1849
    - *Cranchia* Leach, 1817
    - *Leachia* Lesueur, 1821
    - *Liocranchia* Pfeffer, 1884
  - *Subfamily* **Taoniinae** Pfeffer, 1912
    - *Taonius* Steenstrup, 1861
    - *Egea* Joubin, 1933
    - *Sandalops* Chun, 1906
    - *Liguriella* Issel, 1908
    - *Teuthowenia* Chun, 1910
    - *Megalocranchia* Pfeffer, 1884
    - *Helicocranchia* Massy, 1907
    - *Galiteuthis* Joubin, 1898
    - *Bathothauma* Chun, 1906
    - *Mesonychoteuthis* Robson, 1925
- *Order* **Octopoda** Leach, 1818
  - *Suborder* **Cirrata** Grimpe, 1916
    - *Family* **Cirroteuthidae** Keferstein, 1866
      - *Cirroteuthis* Eschricht, 1838
      - *Cirrothauma* Chun, 1911
    - *Family* **Stauroteuthidae** Grimpe, 1916
      - *Stauroteuthis* Verrill, 1879
      - *Grimpoteuthis* Robson, 1932
      - *Chunioteuthis* Grimpe, 1916
      - *Froekenia* Hoyle, 1904
    - *Family* **Opisthoteuthidae** Verrill, 1896
      - *Opisthoteuthis* Verrill, 1883
  - *Suborder* **Incirrata** Grimpe, 1916
    - *Family* **Bolitaenidae** Chun, 1911
      - *Bolitaena* Streenstrup, 1859
      - *Japetella* Hoyle, 1885
      - *Eledonella* Verrill, 1884
      - *Dorsopsis* Thore, 1949
    - *Family* **Amphitretidae** Hoyle, 1886
      - *Amphitretus* Hoyle, 1885
    - *Family* **Idioctopodidae** Taki, 1962
      - *Idioctopus* Taki, 1962
    - *Family* **Vitreledonellidae** Robson
      - *Vitreledonella* Joubin, 1918
    - *Family* **Octopodidae** Orbigny, 1845
      - *Subfamily* **Octopodinae** Grimpe, 1921
        - *Octopus* Lamarck, 1798
        - *Enteroctopus* Rochebrune & Mabille, 1889
        - *Danoctopus* Joubin, 1933
        - *Cistopus* Gray, 1849
        - *Robsonella* Adam, 1938
        - *Scaeurgus* Troschel, 1857
        - *Pteroctopus* Fisher, 1882
        - *Hapalochlaena* Robson, 1929
        - *Berrya* Adam, 1939
        - *Euaxoctopus* Voss, 1971
      - *Subfamily* **Eledoninae** Gray, 1849
        - *Eledone* Leach, 1817
        - *Pareledone* Robson, 1932
        - *Thaumeledone* Robson, 1930
        - *Bentheledone* Robson, 1932
      - *Subfamily* **Bathypolypodinae** Robson
        - *Bathypolypus* Grimpe, 1921
        - *Graneledone* Joubin, 1918
        - *Benthoctopus* Grimpe, 1921
        - *Teretoctopus* Robson, 1929
        - *Grimpella* Robson, 1928
        - *Haptochlaena* Grimpe, 1922
        - *Tetracheledone* Voss, 1955
    - *Family* **Tremoctopodidae** Brock, 1882
      - *Tremoctopus* Delle Chiaje, 1829
    - *Family* **Ocythoidae** Gray, 1849
      - *Ocythoe* Rafinesque, 1814
    - *Family* **Argonautidae** Naef, 1912
      - *Argonauta* Linné, 1758
    - *Family* **Allopsidae** Verrill, 1882
      - *Alloposus* Verrill, 1880
- *Order* **Vampyromorpha** Pickford, 1939
  - *Family* **Vampyroteuthidae** Thiele, 1915
    - *Vampyroteuthis* Chun, 1903

Table 2

Fish Predators of Squid (*Loligo pealei* and/or *Illex illecebrosus*)
from the Northwest Atlantic

	Pelagic		Benthic
bonito	*Sarda sarda*	haddock	*Melanogrammus aeglefinus*
bluefin tuna	*Thunnus thynnus*	cod	*Gadus morhua*
skipjack tuna	*Eughynnus pelamis*	pollock	*Pollachius virens*
mackerel	*Scomber scombrus*	red hake	*Uraphycis chuss*
swordfish	*Xiphias gladius*	silver hake	*Merluccius bilinearis*
		spotted hake	*Urophycis regius*
	Semi-pelagic	white hake	*Urophycis tenuis*
alewife	*Alosa pseudoharengus*	tom cod	*Microgadus tomcod*
butterfish	*Peprilus triacanthus*	searobin	*Prionotus carolinus*
scup	*Stenotomus chrysops*	four-spot A.	*Paralichthys oblongus*
bluefish	*Pomatomus saltatrix*	summer flounder	*Paralichthys dentatus*
striped bass	*Morone saxatilis*	windowpane flounder	*Lophopsetta maculata*
redfish	*Sebastes marinus*	witch flounder	*Glyptocephalus cynoglossies*
	Inshore		
silverside	*Menidia menidia*	barndoor skate	*Raja laebis*
smelt	*Osmerus mordax*	little skate	*Raja erinacea*
		big skate	*Raja binoculata*
three-spine stickleback	*Gasterosteus aculeatus*	clearnose skate	*Raja eglanteria*
weakfish	*Cynoscion regalis*	tilefish	*Lopholatilus chamaeleonticeps*
	Other	longhorn sculpin	*Myoxocephalus octodecemspinosus*
spiny dogfish	*Squalus acanthias*		
smooth dogfish	*Mustelus canis*	white perch	*Morone americana*
mackerel shark	*Lamna nasus*	toadfish	*Opsanus tau*
thresher shark	*Alopias vulpinus*	black seabass	*Centropristis striata*
barrelfish	*Hyperoglyphe perciformis*	goosefish	*Lophius americanus*
angel shark	*Squatina dumerili*	tautog	*Tautoga onitis*
roughtail stingray	*Pasyatis centroura*		

THE CEPHALOPODS: FACTORS RELEVANT TO THEIR POPULATION DYNAMICS AND TO THE ASSESSMENT AND MANAGEMENT OF STOCKS

by

J.F. Caddy
Marine Resources Service
Fishery Resources and Environment Division
FAO, Rome

ABSTRACT

Following a brief review of the cephalopods and their global resource potential, those aspects which are essential to an understanding of their role in the ecosystem, and to the modelling of their population dynamics, and design of research and monitoring systems are briefly reviewed. The methodologies appropriate to assessment of these generally short-lived migratory organisms are looked at and their implications for fisheries management are discussed.

RESUME

A la suite d'une brève étude sur les céphalopodes et leurs ressources potentielles dans le monde, l'auteur examine brièvement les aspects qui sont essentiels à la compréhension de leur rôle dans l'écosystème, à la présentation de leur dynamique de population et à la conception de systèmes de recherche et de surveillance. Il étudie les méthodes qui se prêtent à l'évaluation de ces organismes migrateurs, dont la vie est généralement brève et de leurs incidences sur l'aménagement des pêches.

RESUMEN

Tras un breve examen de los cefalópodos y su potencial global, se examinan sucintamente los aspectos esenciales para comprender su función en el ecosistema, preparar modelos de la dinámica de la población y formular sistemas de investigación y vigilancia. Se estudian las metodologías apropiadas para la estimación de estos organismos migratorios, en general de vida breve, y se examinan sus implicaciones para la ordenación pesquera.

INTRODUCTION

In the early seventies when Voss (1974) prepared his review of world cephalopod resources, it is interesting to note that a major proportion of the world catch of cephalopods (roughly 40 percent) came from the waters of the northwest Pacific around Japan largely as a result of expansion of the Japanese domestic fleet which was already producing over 500 000 t/year as early as 1950 in response to high domestic demand for cephalopods (Hotta, in press). The period of expansion of the Japanese distant waters fisheries for cephalopods documented by Okutani (1977) and by Sato and Hatanaka in this review began in the mid-sixties, and has helped to expand our awareness of the size of this resource on a world scale, a process that is not yet fully complete. In this sense, the Japanese distant water fishery for cephalopods has provided a valuable service to many coastal countries in making them aware, often for the first time, of the presence of these important resources in their coastal waters, and showing them how they can be harvested. As a result, the decline in the Japanese proportion of world cephalopod catches mentioned above (though not necessarily the total amount harvested by Japan) can be expected to continue, as other countries mobilize to fish these resources. Obviously, there are many problems to overcome before we fully understand the life cycles and population interactions of these animals, and it may therefore be premature to make too many generalizations. However, a picture is beginning to emerge which shows how a group of organisms with a completely different evolutionary origin from the marine fish has evolved a quite distinct approach in their population dynamics, in response to the constraints imposed by the common marine environment. Recent interest in the biology and stock assessment of cephalopods has led to a number of studies on these species, of which the preceding papers in this compilation are important examples, and will be widely referred to in this concluding section.

IDENTIFICATION OF CEPHALOPODS

The taxonomy of the Cephalopoda has for a long time been an extremely specialized area of study with its own particular problems. A number of genera and species erected on the basis of material collected during the earlier oceanic expeditions have subsequently been recognized as larval and juvenile stages of other species since collected as adults. The fact that much cephalopod material for identification comes from stomach contents of vertebrates where only the beaks of the jaws remain undigested, also contributes to the problems of precise identification. A large number of taxa are presently of commercial interest[1/]: over 40 members of the order Teuthoidea (squid) are included in the annotated catalogue by Roper and Sweeney (MS)[2/]. Undoubtedly with further fisheries exploration of this underutilized resource, more species (perhaps more oceanic than neritic species?) will be added to this list, particularly since we note that in Japanese waters, where there is a long history of fisheries for cephalopods, at least 20 species (10 of them squid[3/]) are the subject of exploitation (Osako and Murata, this publication): fewer species are fished in most areas of the world, although the number of potentially commercial species present is not known.

The species catalogue of Roper and Sweeney, to be available in 1983, in addition to providing a brief description of the biology, distribution, habitats, fishery and size range of the main species, will contain a key for identification of these resources. This reference will be a useful introduction to the sections on cephalopod identification contained in the FAO Species Identification Sheets (Fischer, 1973). Regional publications in the latter series have already been issued for the Mediterranean/Black Sea (Fishing area 37, 1972), the Western Central Atlantic (Fishing area 31) (FAO, 1978), the Eastern Central Atlantic (Fishing areas 34 and 47 in part) (FAO, 1981), and will soon be issued for the Eastern Indian Ocean/Western Central Pacific (areas 57/71) and for the Western Indian Ocean (area 51).

CEPHALOPOD ABUNDANCE AND POTENTIAL WORLD CATCHES

Various estimates have been made of the abundance and potential catch of cephalopods on a global basis. For example, in 1974, Voss estimated the world catch at between 1.5 and 2 million t, with an estimate of potential catch from shelf and upper slope resources of between 8 and 12 million t. For the oegopsid (oceanic) species, he also estimated potential catches to be somewhere between 8 and 60 times those for the neritic shelf resources, i.e., from roughly the order of size of the present world's fish catch to as high as 500 million t. In absence of fisheries statistics, these extraordinary and

---

[1/] Voss (1974) estimated the number of species of cephalopods in the world's oceans at 650; this figure almost certainly needs revising

[2/] Roper, C.L. and M. Sweeney, Cephalopods of the world - an annotated catalogue of species of interest to fisheries (manuscript currently in preparation for printing)

[3/] Squids are classified into suborders as follows: (a) The suborder Oegopsida, comprising a large number of oceanic species, many of which are not yet commercially exploited, including some which (e.g., the deepwater forms) are never likely to be of commercial interest. This group also contains some of the larger individual marine resources in terms of productivity, e.g., *Todarodes pacificus* and *Ommastrephes bartrami*, and (b) The rather fewer genera of the suborder Myopsida (e.g., *Loligo* spp.) which inhabit the coastal and shelf areas of continental shelves, form an important component of the demersal trawl catch in several areas of the world, as well as being a frequent component of artisanal catches (in retrospect) quite theoretical and tenuous estimates, are derived indirectly from a knowledge of:

(a) the feeding rate of sperm whales (whose diet consists largely of a rather limited number of oceanic squid species), plus estimates of the former size of the sperm whale population, and
(b) the fact that very high concentrations of squid beaks occur in oceanic sediments underlying areas of upwelling and mixing in the tropical oceans, which also coincide with former areas of sperm whale abundance.

Our optimism about the economic and practical feasibility of harvesting or marketing such large resources as are indirectly suggested by the above information may be tempered with more caution than formerly given recent trends in world fuel prices. It is still clear however, that we are dealing with resources, the oceanic squids, which are as yet largely untapped. It should be borne in mind however, that the high productivity/biomass ratio of cephalopods (predicated on their high rate of population turnover or natural mortality rate), may mean that the standing stock that could produce the above production may be significantly lower than for a fish stock of corresponding productivity, so that in fact the proportion of the standing stock found at high enough densities for harvesting to be economically feasible is probably quite low. Further generalization of this "predator-prey" approach however will quickly reveal that cephalopods play a significant role in the diets of many marine mammals and fish species (see e.g., Lange and Sissenwine (1980) for a list of 46 fish predators on squid for a well-studied area - the northwest Atlantic). From similar considerations, Dong (1981) estimates a potentially harvestable biomass of between 5.5 and 7.5 million t of cephalopods from the western Pacific.

Compared with the above potential catch figures, the best estimates of landings (FAO, 1980) seem rather modest (Worms, this review), but show that over the last 10 years, cephalopod landings have been increasing at a faster rate than overall landings for all marine resources.

A comparison of the world cephalopod catches as a proportion of the total catch of all species in each of the FAO marine statistical areas yields some interesting regularities. With the exception of area 81 (New Zealand and the South Pacific, of which more later), the highest proportion of cephalopod catches (Figure 3 in Worms, this review) comes from the northwest Pacific (area 61: 4.7 percent of the total catch), northwest Atlantic (area 21: 4.0 percent of the total catch), and from the Mediterranean (area 37: 3.2 percent of the total catch). Except area 81, all other areas show a low proportion of cephalopods in the catch. On the face of it, therefore, if we could assume that cephalopods are present but not fished in these other areas, we would conclude that the potential yield of cephalopods is of the order of 4 percent of the fish catch, i.e., roughly 2.9 million t, as opposed to the nominal 1981 figures of 1.57 million t. In fact, there are reasons for believing that this is an underestimate, particularly since the key to this potential yield lies with the oceanic squid. These probably could make a significantly greater contribution to world fish landings, perhaps approaching or even exceeding the figure of 12 percent of total landings observed recently in area 81, at least for those open ocean areas situated adjacent to continental shelf zones of high productivity.

It has long been evident, especially from the stomach contents of marine mammals (e.g., Mercer, 1974; Fiscus, 1982) that cephalopods are often abundant in areas where they are not taken by conventional gear. This again argues for more optimistic estimates of potential (e.g., Voss, 1974) than from conventional fishery sources, although it is clear also that more objective estimates of potential yield are now possible than in the mid-seventies as better approaches to assessment of these unconventional resources are being developed.

ASPECTS OF THE BIOLOGY OF COMMERCIALLY EXPLOITED CEPHALOPODS OF INTEREST TO MANAGEMENT

A. Reproduction

Cephalopods occupy a diversity of habitats in the marine ecosystem, from pelagic or semi-pelagic (*Illex*, *Loligo*), demersal (*Sepia*) to benthonic (*Octopus*). Most species appear to lay benthonic eggs, either in large watery gelatinous masses (e.g., *Illex*) within which hatching occurs, in individual yolky egg capsules attached to seaweeds and other branching marine growths (*Sepia, Loligo*), or under rocky outcrops and on other hard substrates (*Octopus*). Brooding of the eggs may occur (as in *Octopus*), so that despite a relatively short free planktonic stage in most cases, the survival of the larvae is probably relatively high. This is almost certainly one reason for the potentially high rates of population increase of cephalopods despite their often relatively low fecundity, ranging from 3 500 to 5 000 eggs in *Loligo pealei*, around 10 000 in *Illex illecebrosus*, 70 000-150 000 in *Todarodes pacificus* and 130 000-250 000 in *Octopus vulgaris*; these animals apparently have found an evolutionary advantage in producing individually relatively fewer, larger yolky eggs ensuring reasonably good larval survival than many marine fish species. This is possibly a consequence of the single spawning season per individual which after completion of all reproductive activities, is often followed shortly afterwards by death of the maternal generation in these animals (see however, Juanicó, this publication). Production of relatively large yolky eggs (and certainly maternal protection of the eggs) confers some advantages in ensuring good individual chances of survival of young, but this is a strategy which, on the face of it, appears more 'risky' than the multi-age annual spawnings of many commercial fish species. For these latter, the continued survival of adults for a number of years following maturity allows at least one successful spawning per year class in an environment which may not be consistently hospitable in each of these years to the environmentally more fragile larval forms. Certainly, in the case of *Octopus*, there is also the advantage of a less pronounced spawning aggregation than for *Sepia*, making the species less vulnerable to heavy fishing during the critical spawning and post-spawning stages. For *Octopus vulgaris*, this is also aided by the solitary 'nest building' activity of females (Hatanaka, 1979) which makes them less vulnerable to trawling at this time of year. Vulnerability of *Sepia* egg masses, as well as for some loliginid squid that spawn in shallow water, may be higher to trawling (FAO, 1971) than for *Octopus* with pre-spawning and spawning aggregations generally occurring often not too far offshore.

The occurrence in recent years of a high abundance of cephalopods in various fishing areas that have recently been subject to intensive industrial fishing, points to the success of their alternative 'life strategy' in environments prone to heavy stress which may be taken to include the ecological impact of heavy fishing. There may in fact be reasons for believing that this strategy is superior to that of longer-lived bony fish under these circumstances. One note of caution must be sounded here however: because of the relatively low fecundity of many cephalopods, too severe a depletion of the current year class may result in an abrupt decline in stock size in the following year: this also seems to have occurred in heavily fished areas.

B. Growth and Ageing

Sampling and size frequency analysis: Although no major problems are presented in measurement of size for cuttlefish or even squid where body form is relatively constant, this is not true for *Octopus*. Body weight is obviously measurable with greater accuracy for this latter species than linear dimensions, but often the catch may be eviscerated or have lost limbs. This latter factor is also responsible for the choice of mantle length rather than total length as a standard measure. It is evident nonetheless from the high variability of mantle length-weight relationships that choosing one ideal size measure for this species is not going to be easy, especially since the most readily available commercial size categories are by eviscerated weight following freezing and thawing. Based on stratified sampling of catches, or on their reconstruction from commercial size gradings (e.g., Pereiro and Bravo de Laguna, 1979 for *Octopus*), modal analysis allows seasonal growth patterns to be obtained, as well as the fitting of von Bertalanffy growth curves, separately by sex.

Growth: As might be expected for short-lived animals where the lifespan rarely exceeds two years, both growth and mortality rates are extremely high. For example, the giant squid, *Dosidicus gigas*, a relatively long-lived species, reaches 20-33 cm by the end of the first year, and 34-45 cm and over 2 kg in weight by the end of the second year (Ehrhardt *et al.*, this publication). The same authors found five separate cohorts were identifiable from polymodal analysis of length frequencies from stocks of this species which enter the Gulf of California annually, each resulting from a separate spawning peak: mature females being found in population samples during most of the year. Each cohort had a different growth rate (reflecting the differing environmental conditions during growth).

In some cohorts growth was roughly linear; in others asymptotic (von Bertalanffy) growth was the case. As noted earlier, for some other species the growth rate shows sexual dimorphism: females often attaining a larger size. The opposite is the case for *Octopus vulgaris* (Pereiro and Bravo de Laguna, 1979) where the males grow faster, and for *Sepia pharaonis* (Sanders, 1981) where, although the females grow faster, like the preceding species, males reach a larger ultimate size and survive longer due to high post-spawning mortality of females. Evidently any careful study of the life cycle of these organisms must take this strong variability of growth into account. O'Dor *et al.* (1980), showed from large tank-holding experiments not only a rigid feeding hierarchy in the school, but also that at a single temperature with unlimited food, weight increase of *Illex* per unit time is proportional to body weight[1/], and more importantly, by comparison with the same cohort sampled in the field, he showed that food availability is the major limitation on growth rate. The effects of small variations in ambient temperature on recruitment biomass and on catch rate and growth are important, but food availability is often a limiting factor for growth, and it was demonstrated that growth becomes more food-limited later on in the season with an associated increase in cannibalism. From this we can conclude that modelling growth by means of the von Bertalanffy equation is doubtful in cases where seasonal limitations in food availability and temperature may be paramount in effect, and both Lange and Sissenwine (this publication) for *Loligo pealei* and *Illex illecebrosus*, and Ehrhardt *et al.* (this publication), for *Dosidicus gigas*, found that growth for some cohorts was best modelled as a linear function of time, presumably under conditions when food availability is not a limiting factor. A more general approach here is that of Mohn (1981).

One other approach to growth and ageing that has been developed in recent years is the use of the calcareous statolith of the squid to estimate growth rates from the number of daily rings present (Lipinski, 1978 and Hurley and Beck, 1980 for *Illex illecebrosus*). A more widespread investigation of the possibilities of this technique in other cephalopods seems warranted. Nonetheless, for new cephalopod fisheries, emphasis should be placed first of all on designing a seasonal sampling scheme for length frequencies in which, say, 100 individuals taken at random from each catch sample are measured, say, to an accuracy (for the smaller species) of ± 0.5 cm (measured for squid and cuttlefish from the antero-dorsal protuberance on the collar, to the apex of the tail fin), and for octopus either the mantle length or total length measured in relaxed condition. Individuals should be subsequently weighed preferably to ± 5 g (especially for octopus which is rather plastic in shape and difficult to measure).

C. Feeding

One other feature that has been described for *Illex* and *Octopus*, and is probably found in *Sepia* and *Loligo* also, is the prevalence of cannibalism in these species. Far from being a counter-productive mechanism, it can be seen that in some circumstances cannibalism provides competitive advantages. This may be illustrated by reference to a pelagic species, such as *Illex*, which initially feeds largely on planktonic marine crustacea (copepods, euphausids, etc.). At a certain point in the life history, the intensive feeding dictated by a high metabolic rate requires a change-over to larger prey items. 'Gaps' in the size spectrum of food in the plankton are now known to be important features limiting survival and year class strength of the larvae of many marine fish species (Jones, 1973). The fact therefore that a wide size range of sizes exists within a single cohort of squid as a result of a pronounced intra-year class competition (O'Dor *et al.*, 1980), the frequent occurrence of a prolonged spawning season, and generally fast growth rates mean that the larger squid can in the temporary absence of other food of the preferred size range, continue to grow by consuming smaller individuals (predominantly males in *Illex*). Thus the faster-growing individuals can make the transition to more abundant, larger prey items higher in the food size spectrum (Amaratunga, 1980). O'Dor *et al.* (1980), in fact concluded from laboratory rearing experiments that growth of *Illex* in the wild is limited by food. In this way, the metabolic gains from consumption of planktonic food by small individuals are passed on to the larger mature individuals in the population, conferring a general resistance to temporary shortage of larger food items to the population as a

---

[1/] On the other hand, an actual loss in body weight can occur if food is very limited whole. The small, but significant proportion (8 percent) of cephalopod items (largely *Octopus*) found in stomachs of *Octopus* off Mauritania, supports this as a potential mechanism for *Octopus*, although the 25 percent fish (especially smaller individuals of *Pagellus*, *Boops* and *Dentex*) and 45 percent crustaceans suggest that the diet of this species is largely opportunistic (Nigmatallin and Ostapenko, 1976). The impact of a cephalopod population on its ecosystem must also be considerable; from tank experiments on *Illex*, in which an *ad libitum* feeding regime was maintained, O'Dor *et al.* (1980), estimated that roughly 5 percent body weight was consumed per day, resulting in growth rates of roughly 1.5 percent body weight per day, i.e., an efficiency of conversion of food to body tissue of around 30 percent was observed (which is relatively high) while daily feeding rates as high as 12 percent for *Octopus* and 30+ percent of body weight for juvenile *Sepia* are summarized in Conover (1978). If cannibalism is prevalent in the population, of course the net efficiency of transfer of biomass from the trophic level below to the one above will be much reduced. Nonetheless, if continued uniformly for 360 days at 5 percent body weight per day with 30 percent efficiency, a squid of 1 g initial weight would attain 213 g at the end of the period by consumption of a calculated 716 g of food. Although these figures will not apply exactly in the wild, they do illustrate that a population of, e.g., 100 000 t of squid (even allowing for some cannibalism) will have consumed on reaching harvestable size several times their present biomass of other organisms, including a significant proportion of juvenile fish. Their potential impact on recruitment of other species is fairly evident from this, and deserves more careful investigation.

D. Intraspecific Interactions Cannibalism and the Stock Recruitment Question

It may be worthwhile to note here that many organisms in the marine food web occupy more than one adjacent level in the trophic pyramid during their life history. There is a general tendency for that small proportion of the primary production of plant material incorporated into animal tissue to move upward in the trophic pyramid by either predation (interspecific transfer) or by metamorphosis or change in diet (intraspecific transfer). A large proportion of the original food consumed is lost by respiration and excretion at each step upward in the food web. Squid illustrate both of these mechanisms intraspecifically: the smaller oceanic squid and juvenile stages of other cephalopods feed on planktonic organisms, but often make a transition to a diet of fish or squid later in life. As noted in the last section, the apparently widespread occurrence of cannibalism in squid (e.g., *Illex* (Amaratunga, 1980), *Dosidicus* (Ehrhardt *et al.*, this publication), may represent a mechanism for ensuring that the genetic material essential for stock replenishment in an annual species with a single spawning per individual in its lifetime, makes a successful transition from a planktivorous mode of life to higher order predation (piscivory) in an uncertain environment. In situations where high temporal fluctuations in food availability occur (e.g., close to continental shelves showing high seasonal fluctuations in productivity), a temporary unavailability of larger prey (e.g., juvenile fish) at this critical point in the life history could have serious effects on survival to spawning, and a greatly diminished recruitment the following year. Seen from this point of view, the following features of various cephalopod life histories appear adaptive:

1. A prolonged spawning season or a series of intra-annual cohorts (e.g., *Dosidicus gigas*, Ehrhardt *et al.* (this publication)), appear to allow the population as a whole to function at more than one trophic level simultaneously, with transfer of biomass between these levels by cannibalism.

2. The relatively large size of prey relative to body size (food is held and shredded by the beak and radula before consuming) allows predation on other individuals even in the same cohort (the upper limit of prey size is roughly equivalent to the mantle length in *Illex* (O'Dor *et al.*, 1980); a mechanism that is facilitated by sexual dimorphism in growth of some species (e.g., *Illex illecebrosus*, where preferential consumption of the smaller males occurs).

3. The suggestion has been made for *Todarodes* (Osako and Murata, this publication) that a series of individual spawning areas, substocks or 'stocklets' may occur in sequence along the continental margin or slope, each benthic breeding area associated with a particular feature of the continental slope (e.g., canyons or sea mounts). The identity or degree of genetic isolation of these 'stocklets' is unknown, but the fairly wide latitudinal range of, e.g., *Illex illecebrosus* and *Illex argentinus* may mean that this provides

another 'fall-back' mechanism for subsequent 'lateral recolonization' in the case of local recruitment failure. The suggestion has been made (Doi and Kawakami, 1979, for *Todarodes pacificus*) that despite a wide diversity of identifiable cohorts throughout the range of the species, here (and presumably also for other such species) we are dealing essentially with a single population species with wide diversification and plasticity in growth form and timing between subcohorts.

Spawner-recruit mechanisms. Apparently reasoning largely from theoretical considerations, Au (1975) concluded that since stock recruitment relationships of the Ricker type imply a degree of intraspecific (intergeneration) competition that cannot easily occur in annual species that die soon after spawning, the type of asymptotic stock-recruitment relationship postulated by Beverton and Holt (1956) is more likely to occur. Certainly, a spawner-recruit relationship of this type appears to be in accord with the rapid increases in stock size observed, despite a frequently rather low individual fecundity, fairly high survival from generally large yolky eggs, and a single female spawning per life cycle. On the other hand, the widespread occurrence of cannibalism, in addition to its other possible significance mentioned above, could also act as a density-dependent population regulation device that comes into play more strongly when other food supplies are limiting, such that all other external trophic factors being equal, individual survival may be reduced in times of high recruitment. This would tend to produce a dome-shaped type of spawner-recruit model if recruitment success is made a function of initial biomass or stock size the previous year. Such a model has been reported on in the review of Japanese literature by Osako and Murata (this publication). Another possible mechanism that could lead to a Ricker type of spawner-recruit relationship could be a limited availability of suitable safe spawning areas. Where egg laying occurs in crevices (e.g., for *Sepia* and *Octopus*), the occurrences of suitable shelters could, as for the classic example of a Ricker spawner-recruit model, the salmon, be a limiting factor or reproductive success.

In actuality, if cephalopods are regarded as opportunistic 'r-strategists' (see later), filling temporary niches until cropped down by predation pressure, the argument between these two types of spawner-recruit curves may be largely academic, since the population will spend nearly all of its time on the ascending side of the S-R curve where the two models are indistinguishable.

It may be noted however (see Sato and Hatanaka, this publication, for details), that the Beverton and Holt spawner-recruit relationship has been used as the basis for a supposedly optimal exploitation rate of E = 0.4 for *Illex illecebrosus* (and by extension, for other stocks also). This may in practise be a reasonable rate of harvesting for cephalopods, but it must be noted that there is little hard evidence supporting this now conventionalized rate of fishing.

E. Migration and Stock Forecasting

For most cephalopods, but particularly squid, one or more migratory phases during some state of the life history is characteristic. Even for octopus species, vertical migrations for spawning purposes may coincide with periods of particular vulnerability, e.g., *Octopus dofleini* around Hokkaido (Osako and Murata, this publication), and this is also true for cuttlefish, which seasonally may occupy relatively restricted spawning grounds close to shore (e.g., *Sepia pharaonis*, Sanders, this publication; *Sepia officinalis hierredda*, Bakhayokho, this publication). This appears also to be true for such species of myopsid (neritic) squid as *Loligo pealei* (Lange and Sissenwine, 1980) which migrates on and offshore, covering distances of as much as 200 km seasonally. This species shows a tendency in its seasonal distribution to follow a relatively limited range of temperatures, which in the case of *L. pealei* takes it from close inshore to 200 m depth in winter in order to remain above the 8°C isotherm. This behaviour is seen on a broader scale for some of the important oceanic squid where the distribution range is often wide (e.g., *Ommastrephes bartrami*, Osako and Murata, this publication) where the fishery extends across 100° longitude, effectively the width of the Northern Pacific, but here is closely correlated latitudinally with key oceanic 'fronts' between adjacent water masses. This species shows a characteristic of many oegopsid squid, namely a tendency to be distributed in relation to major oceanic current systems and close to the boundaries of water masses with different temperature or other hydrographic characteristics. As noted by Grandperrin (1978), the boundaries or fronts between adjacent current systems are often areas where upwelling of nutrient-rich water may lead to oceanic production being initiated or accumulated. Another example is the fishery for *Nototodarus* spp. in New Zealand waters, which has recently been found to depend on two closely similar species (as yet unclassified), each associated with a different water mass (Smith, Roberts and Hurst, 1981): the western type of *Nototodarus* in subtropical water, and the eastern type around the subtropical convergence zone and in sub-Antarctic water[1/]. The life cycle of many of these oceanic squid must also be carefully tuned to the movements of the water masses themselves. In fact, information on oceanographic parameters or 'fronts', together with early season pre-recruit, and early recruit occurrence in research surveys, and as by-catch in other fisheries are important indicators used by domestic Japanese fisheries agencies in their rather accurate forecasts of the time, place and abundance of occurrence of several species of oceanic squid in the North Pacific. For winter populations of *Todarodes pacificus*, for example (Osako and Murata, this publication) larvae from the main spawning in the East China Sea in June-March are carried northward by the Kuroshio current, and larvae from other spawnings to the Japan Sea with the Tsushima warm current. A reverse southerly 'countercurrent' migration of premature adults is again associated with hydrographic conditions, a pattern that occurs for other species associated with major oceanic systems (e.g., spiny lobsters). This must be a necessary mechanism in order to solve the problem of returning the spawning adults to a point in time and space such that their passively drifting larvae arrive at the same adult feeding grounds as the previous generation.

Bear in mind that there will be three phases in most fisheries for migratory species:

(a) Immigration to the fishery (often combined with a period of partial retention by the gear);
(b) A period of relatively constant availability to the fishery, and
(c) A period of emigration, when availability to the fishery declines.

Caddy (1979) proposed an approach to analysis of population trends based on the assumption that these three phases can be recognized from either:

- analysis of catch rate trends;
- cohort analysis, assuming constant M and availability (when onset of immigration and emigration phases will be recognizable as inflexion points in the series of mortality rates or log numbers calculated for each short interval, Figure 1), or
- from an examination of the sex ratio and average position of samples on the species maturity scale (Juanicó, this publication), remembering that gonad maturation and presence of mature spermatophores may immediately precede the emigration phase.

Having demarcated the characteristics of the onset of full availability and of emigration, we can then formulate expressions for the apparent mortality rate per short unit of time in each phase, noting that 'Zs' for Phases I and III will be biased since for:

Phase I $'Z_I' = q_1f_1 + M_1 - I$

Phase II $'Z_{II}' = q_2f_2 + M_2$

Phase III $'Z_{III}' = q_3f_3 + M_3 + E$

where I and E are rates of immigration and emigration (assumed exponential), and only in Phase II does Z_{II} reflect true mortality, i.e., the sum of natural mortality M and fishing mortality (qf). Thus, any analysis of the rate of fishing by means of Leslie-Delury methods (see Ricker, 1975) should only be applied to data from Phase II of the fishery.

[1/] Interestingly enough, the two species could be distinguished by incidence of parasites and by electrophoresis, as well as from morphological characteristics, suggesting that these methods could have a wider application for cephalopods, as they already have for marine fish species

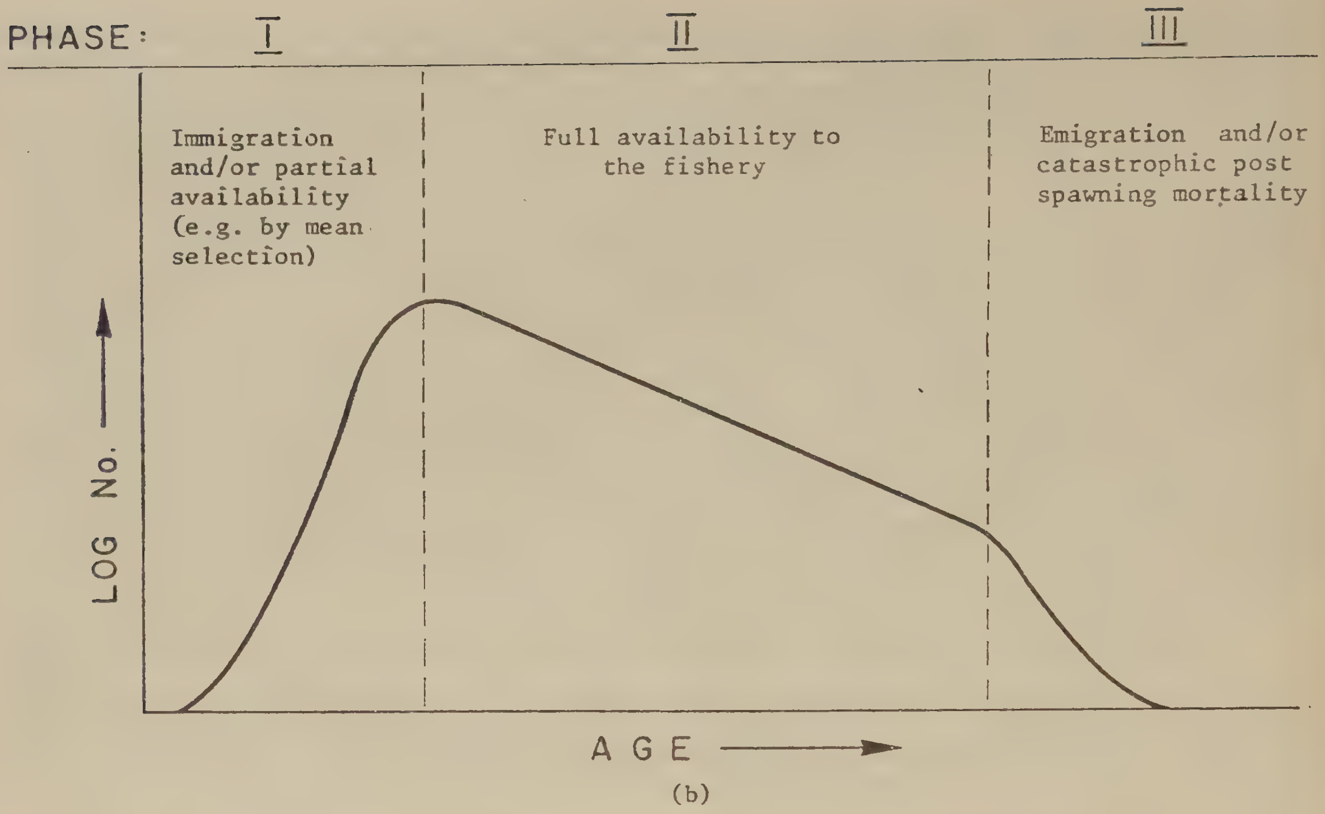

PHASE:
I
II
III
Immigration and/or partial availability (e.g. by mean selection)
Full availability to the fishery
Emigration and/or catastrophic post spawning mortality
LOG No.
A G E
(b)

Figure 1 Diagrammatic illustration of life cycle in an exploited cephalopod life history, showing a simplified representation of three stages passed through by many cephalopods prior to, during and subsequent to full commercial exploitation

F. Interspecific Relationships between Cephalopods and Other Components of the Fisheries Ecosystem

There is growing evidence that the development of large fisheries for cephalopods can occur in areas where past heavy fishing has reduced stock sizes of marine fish species. In some cases this phenomenon can only be guessed at, since poor information exists on the abundance of these species prior to the development of specialized fishing methods, and specific statistics on their capture prior to commercialization. For at least two areas however, there seems to be an adequate data base to document this phenomenon: for the Gulf of Thailand trawl fishery, and for the Mauritanian fishery for mixed demersal species.

G. Interactions between Fisheries for Different Species: the Mauritanian Trawl Fishery

One example of a rather dramatic increase in availability of cephalopods in a mixed trawl fishery is provided by the recent fisheries for *Octopus* off the Western Sahara. It is quite clear from a number of sources of information, not all of them quantitative, that there have been dramatic changes in the trawl fisheries off the Western Sahara over the last two-three decades. Early Spanish exploratory fishing in the forties found negligible quantities of cephalopods in what must have been a fishery dominated largely by sparids (judging also from the frequency of Spanish place names in the area which refer to sparids, and where now sparids are reported to be rare or infrequent!).

Spanish trawl catches of cephalopods in a predominantly sparid fishery were negligible off the Sahara coast in the forties (Navarro *et al.*, 1945). However, evidence summarized by the CECAF Working Party on Regulatory Measures for Demersal Stocks (FAO, 1970) showed clearly that sparid catch by all foreign fleets fishing the CECAF area had dropped off to low levels over the period 1962-69. Catches of the Polish fleet reflect this well (Figure 2A), but more convincing evidence comes from a series of research cruises over the

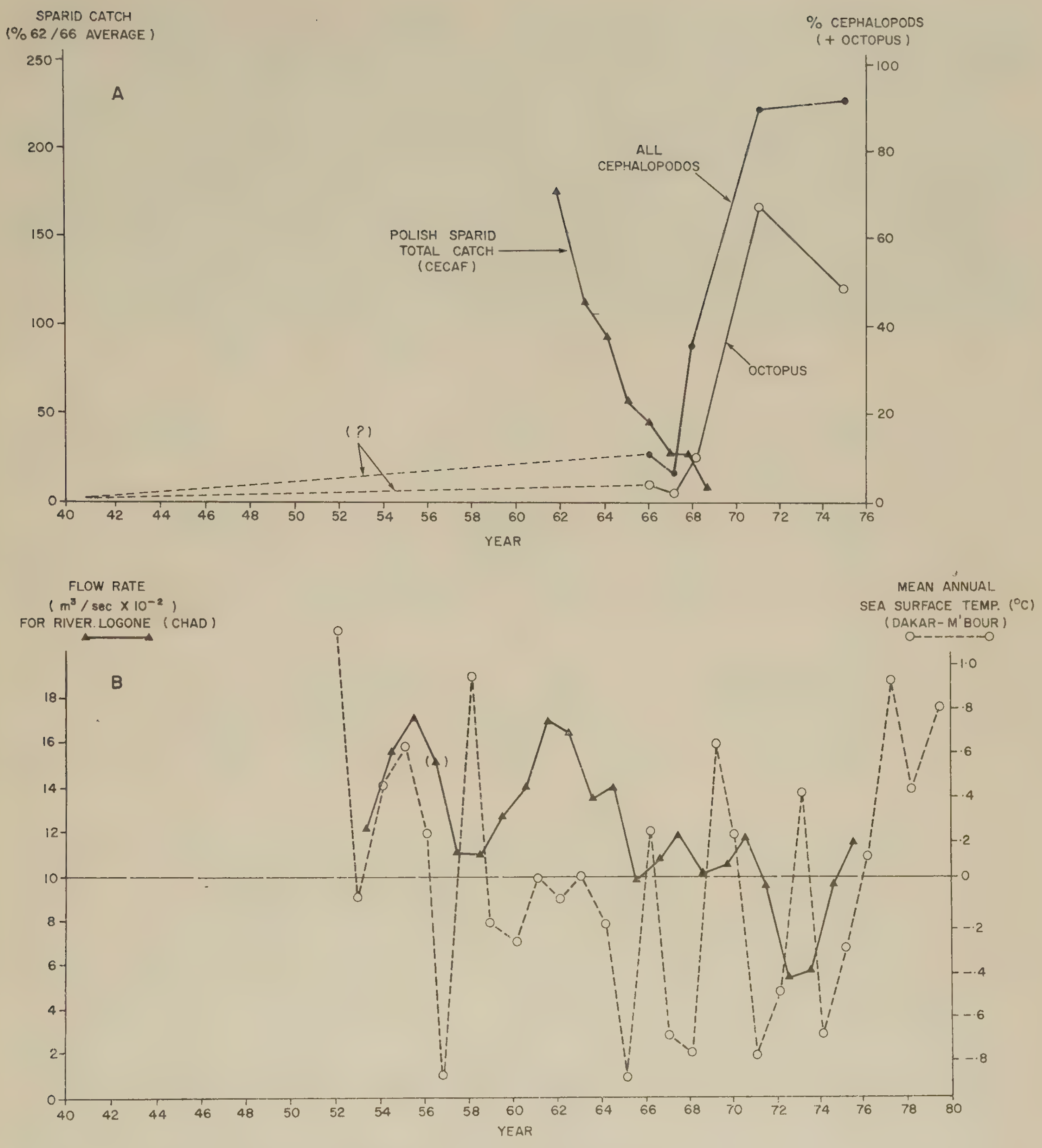


Figure 2 A. Resource trends for the Western Sahara trawl fishery since 1940 (based on research vessel results and commercial catches)

B. Two series of environmental data showing that environmental conditions have not remained constant in recent years in, or off the coast of Northwest Africa period. Beginning in the late sixties, however, catches of cephalopods began to increase: first of all, *Sepia* was a major catch constituent, to be followed later by *Octopus* as the dominant organisms in research vessel and exploratory fishing catches (Figure 3).

Surveys by the N/O THALASSA in 1962 showed only 3 percent of the cephalopod catch consisting of *Octopus* (Pereiro and Bravo de Laguna, 1979), and in his paper subtitled "Cephalopods as by-catch", Klimaj (1970), reporting on the results of the 1966 Polish surveys around Cap Blanc, noted that *Octopus* made up 3.9 percent of the 12 percent by-catch of cephalopods (mostly *Sepia*). In 1968, however, the N/O THALASSA found that 10 percent of the 36 percent of cephalopods taken on the same grounds consisted of *Octopus*, while in 1971, 90 percent of the commercial catch consisted of cephalopods, and 75 percent of this was *Octopus* (Pereiro and Bravo de Laguna, 1979). Finally, in 1975 the Spanish trawl fleet on the Sahara grounds took 90 percent cephalopods, of which 49 percent were *Octopus* (Bravo de Laguna *et al.*, 1976).

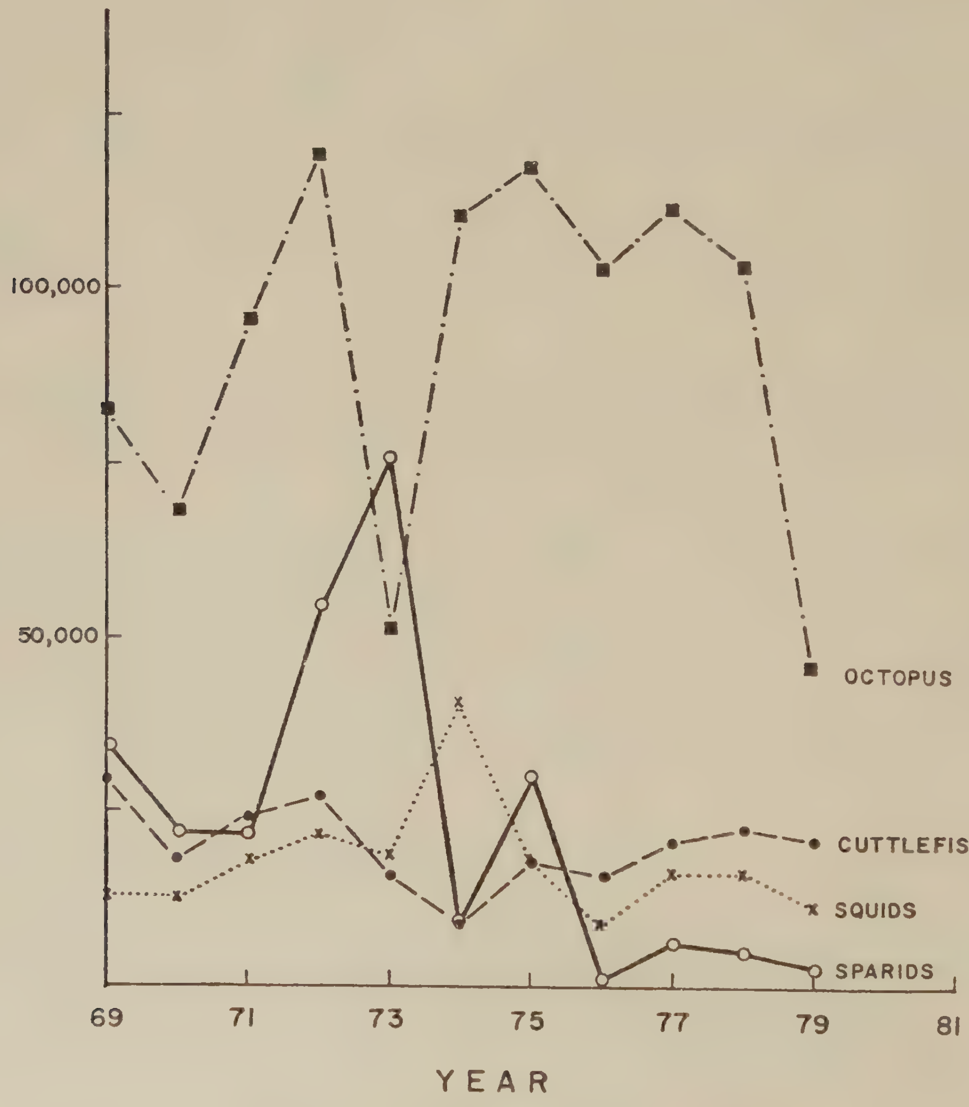


Figure 3 Catch trends in the trawl fishery (Sahara coastal division), since 1969 for three cephalopod species, and for sparids

This transition in dominant species over a 5-6 year period (Figure 2) is not easy to explain in terms of classical population dynamics theory, which in general is based on the assumption of environmental stability and constant carrying capacity for the commercially exploited species. We may postulate that these changes are in part due to changes in the type of fishing gear being used and the method of fishing which in turn may have been initiated by a change in relative market values of sparids and cephalopods. This is not totally convincing, however, since 'pulpo' (*Octopus vulgaris*) has always been a sought-after species in Spain, but was a negligible by-catch of the traditional Spanish sparid fishery in the area before 1966. Also, although the Japanese fishery was initially for sparids, octopus were always a high value species in Japan and certainly would not have been discarded. Thus, although the gear type now in use by the Japanese to catch cephalopods has changed (a high aperture overhanging headline trawl is now in use, towed slowly (2 kn) and especially designed to catch octopus with its rapid escape movements), there is still considerable doubt that this entirely explains the transition in dominant species; especially the exploratory and research vessel results.

We may conclude that there is evidence for a transition between a largely sparid-dominant community to one in which the commercial resources are largely dominated by cephalopods, especially *Octopus*. Similar abrupt transitions, especially in the face of heavy fishing, have been noted in other parts of the world, although it is far from clear yet to what extent they have been entirely a result of fishing as opposed to an effect of environmental fluctuations. This is again true here, since we can also produce evidence from around the world for environmental changes favouring one marine community or species over another. An example here is the *Illex* squid fishery of Eastern Canada (Figure 4) (Rowell, pers. comm.). A large part of the 100-fold changes in biomass here over a 10-year period appear to be associated with climatic changes.

That there have also been significant changes in climate in the North Central African continent over the last few decades cannot be doubted: changes in the upwelling regime associated with changing frequency and strength of offshore winds have been noted over the short term by oceanographers and the recent drought in the Saharan region is well documented, and undoubtedly this is also associated with direction and strength of prevailing winds.

Figure 2B shows two of the few long-term measurements of climatic variables I was able to find: river flow rates from a well-studied area near Lake Chad (Durand, 1978) and annual mean surface temperatures off Dakar-M'bour (Hisard, pers. comm.). I stress that no attempt is being made to suggest that river flow rates in Chad are in any way related casually to cephalopod production in West Africa! We may however feel more confidence in suggesting that surface temperatures off Dakar will influence, or (less emphatically) will be correlated with changes in local fish production. What is being illustrated here is simply that marked climatic changes took place in North Africa over the period of species transition noted above. Both series of environmental data, although selected at random, illustrate this point. In a general sense, although their cross correlation is not significant, both indices also appear to show above average values for the early years (1953-56) and below average values for 1971-75, corresponding to the periods of sparid dominance and cephalopod dominance, respectively. Since many environmental variables are closely cross-correlated and geographically of wide extent, reduced runoff from coastal rivers, upwelling indices, or mean environmental temperature, for example, are all likely to be interrelated to some degree; in particular, the direction and strength of prevailing winds in a given year is likely to be related both on the one hand to precipitation, and on the other to the extent of coastal upwelling.

Do environmental variables influence the equilibrium between different species in an ecosystem and, if so, how? While we can answer the first question affirmatively from a vast amount of human experience on the subject, we cannot answer the second without a great deal more research. We can, however, postulate some experimental observations. For example, noting that in 1976-79 the mean surface temperatures returned to the mean values observed in the early fifties when cephalopods were less abundant, we can await with interest to see what will be the effect of this on the size of the resource. Of course, a decline in cephalopod stock size or recruitment from 1980 onwards would help support the environmental hypothesis, but would not entirely rule out the synergistic impact of heavy fishing. If there is not such a decline, however, one would be more inclined to believe that the decline in sparid abundance was the main factor governing increase in cephalopod stock size in the late sixties, and not climatic change.

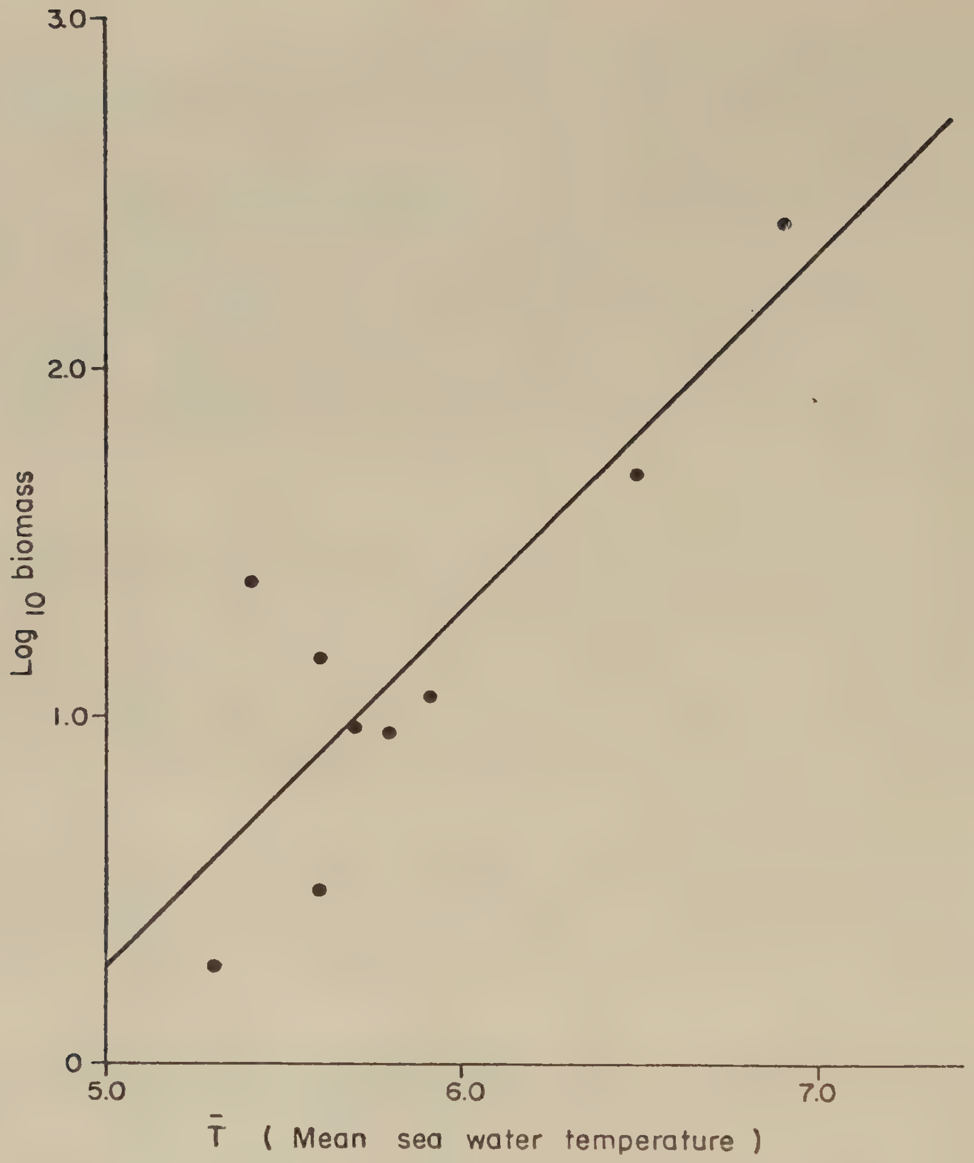


Figure 4 Postulated relationship between annual biomass on the shelf and mean seawater temperature for *Illex illecebrosus* on the Canadian east coast (Rowell, pers. comm.)

Evidently the conventional explanation of species transition as a result of fishing alone is not entirely satisfactory. For example, if we were to assume simple Schaefer models for a finfish species and a cephalopod species in the same fishery, with equal vulnerability to fishing, we could have suggested that since cephalopod population growth rates and natural death rates are generally higher than for most bottom fish of the sparid type, and since it is usually postulated that $M \cong F$ at the level of effort (f_{MSY}) that gives the highest production for the species, the two maxima would occur in succession: cephalopods taking over from sparids as the fishing grew more intense (Figure 5). Superficially, this is somewhat convincing, but cannot provide a full explanation in this case, since we are forced to conclude under this model that there was already a significant proportion of cephalopods in the fishery in the forties and fifties. This appears not to be true judging from commercial catches and research vessel survey results (Figure 2A). One other indication that this hypothesis is simplistic, is the fact that subsequent replacement of squid and *Sepia* in the fishery by *Octopus* is in the contrary direction to what would be expected if species replaced each other in order of their natural mortality rate.

An alternative, and more reasonable, explanation must be based on better knowledge of the ecological role of cephalopods. A review of this subject follows in the next section.

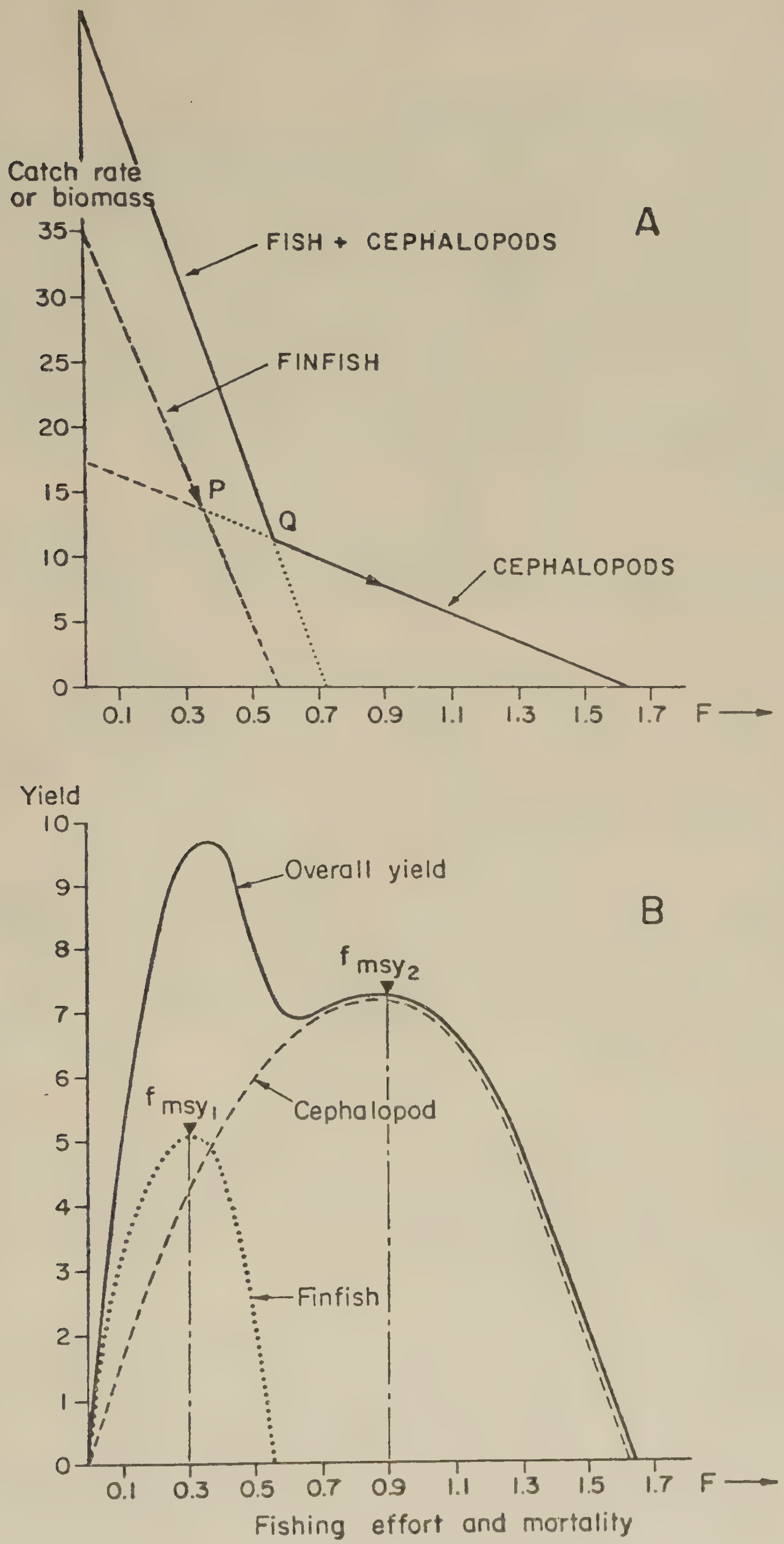


Figure 5 Diagrammatic illustration of the transition between a finfish dominant fishery to one dominated by cephalopods, assuming the simplistic hypothesis of two Schaefer models without biotic interaction, and where $F_{MSY} \cong M$. Between P and Q a transition from a fishery aimed at fish to one aimed at cephalopods is postulated. This modelling approach does not seem to explain the features of many species transitions.

SPECIES INTERACTIONS AND FISHERIES MANAGEMENT

The ecological interactions that are implied if not identifiable in detail in the above example seem also to have some general implications elsewhere in world fisheries where cephalopods are now a significant catch component. Similar evidence for an increase in cephalopod (largely squid) abundance following onset of intensive fisheries for finfish appears to exist for the Gulf of Thailand (Pauly, 1979). Other regions such as the Mediterranean and around Japan where groundfish resources have been subject to a heavy fishery for many years, also demonstrate a high proportion of cephalopods in the catch. However, as with other sea areas (e.g., the Northwest Atlantic) where there are now large cephalopod fisheries, the records of relative abundance of cephalopods and commercial fish species rarely go back far enough in the history of exploitation, so that it is impossible to say whether the increases in squid and cuttlefish landings that have occurred in most areas of the world (see Figure 3 in Worms, this publication), are a result of an absolute increase in abundance, or an increase in marketability.

Trying to define more precisely the mechanism underlying interactions between different species in ecosystems is one of the major preoccupations of fisheries scientists at the moment, and has direct management implications as noted in this quotation from a US Fishery Manager, S. Appolonio:

"A better understanding of the way the system works is clearly needed. The recent emphasis on quantitative assessments as the basic management tool has not been very helpful to managers because assessments contain little predictive content... Perhaps a more qualitative understanding - which I believe is possible - of the characteristic functions of the system would be more useful for managers and less expensive. A manager frequently is not primarily concerned with an accurate estimate of the abundance of a stock. He is more likely concerned with a probable trend of relative abundance."

Bearing this point of view in mind, Figures 6A and 6B show a diagrammatic and undoubtedly very much simplified schematic diagram of the role of coastal squid stocks in the fisheries food web of the continental shelves and adjacent slop waters. Based on observations from several sources, e.g., *Illex* (Amaratunga *et al.*, 1979), *Loligo* (Vouk, 1972), *Todarodes* and *Ommastrephes* (Osako and Murata, this publication), this schematic food web places the squid in an ecological context that may still be useful to managers even though no quantitative predictions can be made from it. (See e.g. Saila and Parrish 1972 for a more formal approach: "graph theory").

The trophic pathways suggested in Figure 6 are generally supported by the limited information available, but the rate of biomass flow (shown by the width of the arrows), as well as the key trophic pathways postulated as control mechanisms for the system (implied by the shaded arrows) are hypothetical. This figure does however provide a conceptional model and working hypothesis which would account for an increase in squid abundance following heavy exploitation of the fish resources of the continental shelf. Expressed in words, the postulated mechanism is as follows:

It is presumed first that the amount of biomass passing from one ecosystem component to any predator is not necessarily the only measure of the degree of control reciprocally exerted by that predator on its prey, since this will depend also on the size of the prey population and the proportion it makes up of the predator's diet (itself often a variable quantity). Thus, the egg and larval stages of a given species may be a relatively minor component of the biomass consumed by planktivorous fish, but such species have been postulated to exert a significant influence on the recruitment success of the prey species, acting through the larval stage (an example for fish stocks is given in Lett, Kohler and Fitzgerald, 1975). In the situation depicted in Figure 6A, three components, each having a high intrinsic production rate, namely zooplankton, benthos and in some cases, mesopelagic fish, may each form large components of cephalopod diets, but we would rarely be aware of any reciprocal impacts of squid feeding on these components, even should they exist. It is postulated that the major exploitable components of the biomass prior to onset of fishing consisted of piscivorous fish (secondary and tertiary predators) feeding among other things on adult squid, and the larger biomass of planktivorous and benthic

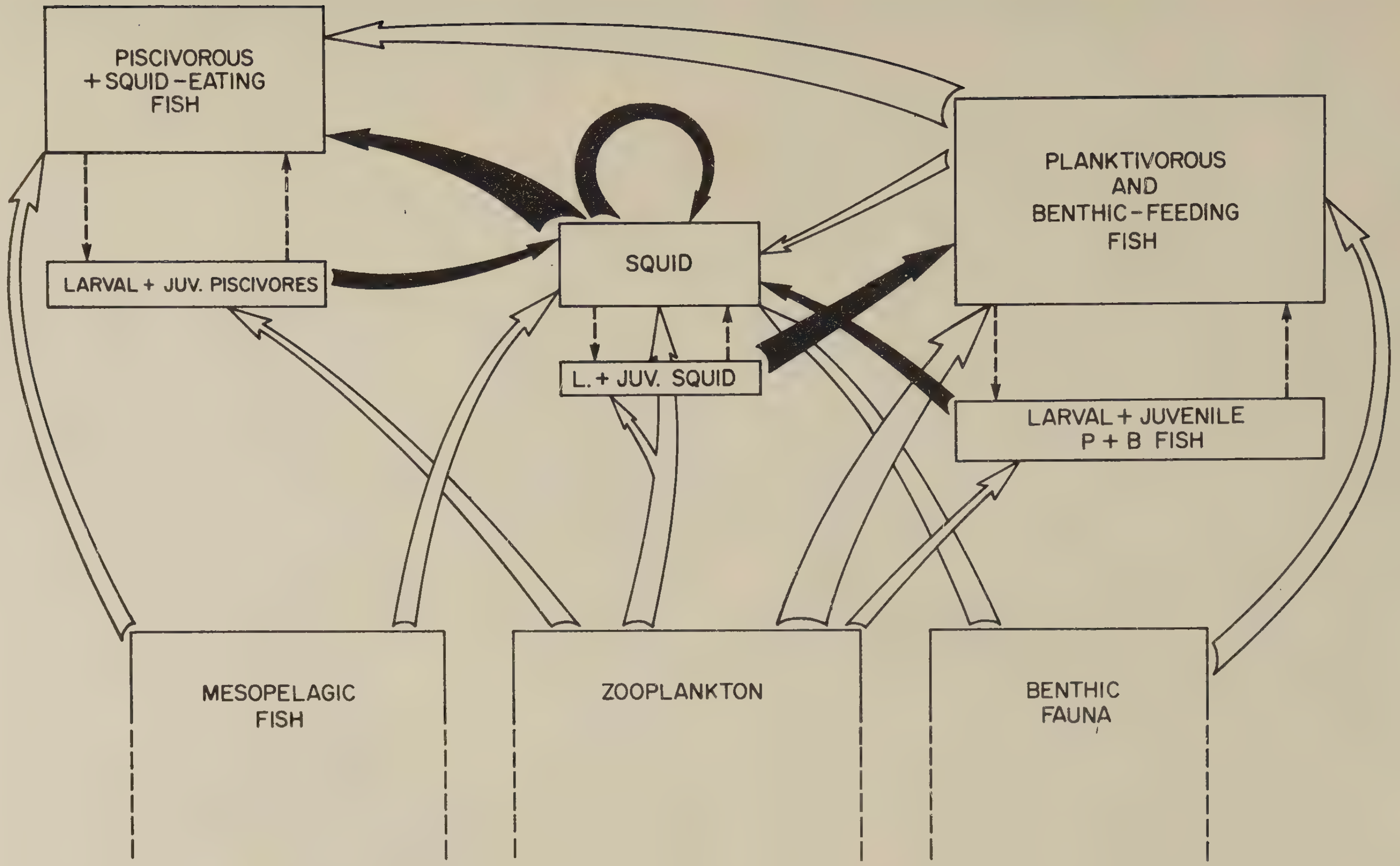

PISCIVOROUS
+ SQUID - EATING
FISH
LARVAL + JUV. PISCIVORES
SQUID
L. + JUV. SQUID
PLANKTIVOROUS
AND
BENTHIC - FEEDING
FISH
LARVAL + JUVENILE
P + B FISH
MESOPELAGIC
FISH
ZOOPLANKTON
BENTHIC
FAUNA

Figure 6A Hypothetical trophic interrelationships of neritic squid in the marine ecosystem prior to intensive fishing on any of the components

Key: Outlined arrows indicate direction of flow of biomass; dashed arrows imply intra-specific stock-recruitment; thickness of arrows corresponds to presumed importance of control exerted by predators on prey biomass; black arrows are those presumed to be of key importance in determining relative abundance of squid and marine fish components of ecosystem (excluding mesopelagics)

The size of boxes is roughly related to the biomass of the components. The three basal components are left open to imply that they are probably large in biomass, and relatively independent of all but major changes in the upper components. Circular shaded arrow above squid box implies cannibalism

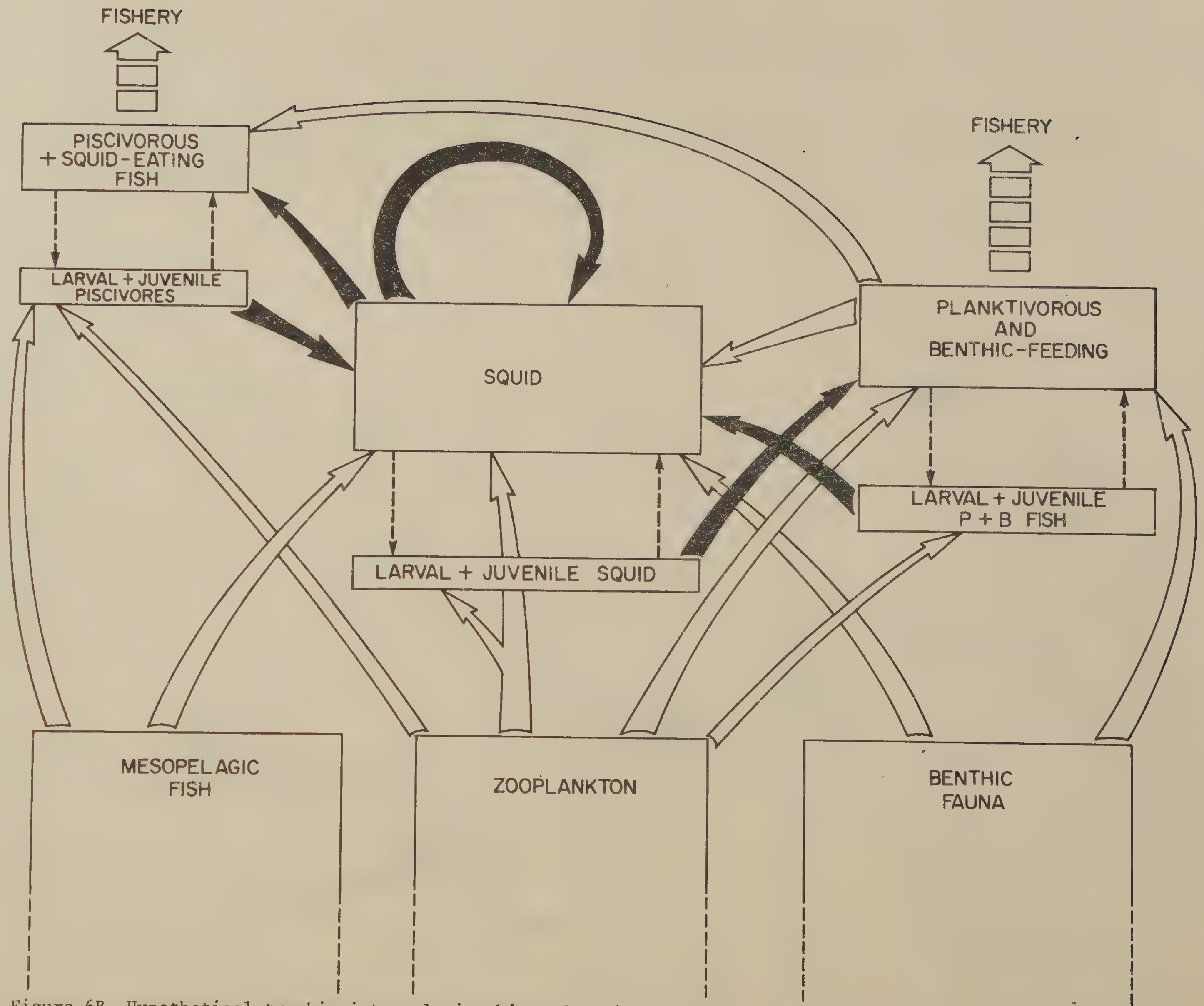

FISHERY
PISCIVOROUS + SQUID-EATING FISH
LARVAL + JUVENILE PISCIVORES
SQUID
LARVAL + JUVENILE SQUID
FISHERY
PLANKTIVOROUS AND BENTHIC-FEEDING
LARVAL + JUVENILE P + B FISH
MESOPELAGIC FISH
ZOOPLANKTON
BENTHIC FAUNA

Figure 6B Hypothetical trophic interrelationships of squid in the marine ecosystem after intensive fishing on marine fish components of the ecosystem, and prior to an intensive squid fishery

Key: Same as for Figure 6A

feeding fish, consuming among other things, larval and juvenile squid. Presumably some uneasy equilibrium[1] between the biomasses of these components occurs in the unfished state, and it is supposed that with the onset of intensive fisheries (at first only on the fish components), this balance was disrupted, with the result that a transition to a situation like Figure 6B may then occur. It seems plausible to suppose that an increase in squid biomass relative to that of fish may be perpetuated while cephalopods remain unexploited, since presumably the controls on fish recruitment by squid (arrow A) may be more intensive, and by fish on squid recruitment and survival (arrows B and C) less so. Based on this qualitative conceptual model, we may make a prediction that the onset of an intensive squid fishery should be the main factor permitting the former ecosystem balance to be restored, if this is a desirable objective. On this question however, we can make the analogous point made with respect to finfish by-catch in penaeid trawl fisheries (Caddy, 1982), that since in general, penaeid shrimp, squid and other short-lived invertebrates have higher growth and natural death rates than most fish, then if catchability is comparable between fish and invertebrates, the sequence of disappearance of each species from a mixed fishery will be roughly speaking, inversely related to its natural mortality rate, especially if size at first capture exceeds size at maturity. This much simpler mechanism which is independent of trophic considerations is an alternative to the one proposed above, and strongly suggests that any attempt to adjust the balance in favour of fish biomass must employ a method of fishing which is very selective for cephalopods. Fortunately, such fishing methods exist for squid (Okutani, 1977): e.g., jigging and for pelagic species, surface gillnets. Evidence even exists (Osako and Murata, this publication) that intensive fishing effort can result in a serious decline in stock size of cephalopods (e.g., *Todarodes pacificus*, around Japan over the last decade) although here again, as for the sparid-octopus example mentioned earlier, long-term climatic influences cannot be excluded.

In this context, it may be useful to regard squid as belonging to the category of r-selected species (MacArthur and Wilson, 1967): opportunistic species with a high natural rate of increase, which are able to expand rapidly in population size to fill vacant niches in the ecosystem left as a result of perturbations (natural or man induced) that have reduced the numbers of trophically more specialized, slower-growing and reproducing, K-selected species. From this point of view of the marine ecosystem, heavy fishing may be regarded as an unbalancing phenomenon on the food chain, since as noted by Garrod (1973), "different rates of exploitation in the components of a multiple resource... imply non-equilibrium conditions in the individual stocks."

ASSESSMENT OF SQUID STOCKS

Although to a considerable degree, the problems of assessing and managing cephalopod stocks are similar to those faced with respect to conventional fish resources, there are some additional problems resulting both from our relatively poor knowledge of the biology of these resources, and perhaps more seriously, from the short life-span of most cephalopods. This short life-span means that in contrast to conventional multi-age structured resources, effective 'real-time' management measures in response to, for example, serious declines in catches and population size, which would have to have a response time of less than one year. This rapid response would be essential to real-time (e.g., quota) management, unless a scheme can be developed that is to some degree a self-correcting one, or which minimizes the disruptive effect of poor short-term decisions. Current stock assessment theory was developed for multi-age structured fish resources, where one age group may take part in the fishery for two, three or more years. This degree of continuity allows some safety margin in the management process, in that because one is dealing with the same group of individuals for several consecutive years, errors in estimates of population size and fishing intensity on a given year class in its first year in the fishery can be corrected for and refined by subsequent analysis of successive annual catches from it. Errors in the amount of removals from a given year class can thus to some extent be corrected by actions in subsequent years, to ensure, for example, that a sufficiently large spawning stock has one or more chances of reproducing itself over the mature part of its potential life-span. In the case of most cephalopods, this continuity is reduced (for species like *Octopus* that only survive three to four years in the fishery, and for *Sepia* which spends about two years in the fishery), or lost entirely for species like *Illex* which basically have an annual, or at most biennial, life-span, growing rapidly to maturity, reproducing and dying shortly afterwards; especially the females. This has been documented for squid and cuttlefish and has also been suggested for female octopus.

---

[1] The sensitivity of cephalopods to climatic fluctuations and their short life history means that more rapid changes in stock size from year to year may occur than for multi-age species. Under these circumstances, the concept of a fishery-induced successional change in an exploited ecosystem (Odum, 1965) may prove to be more relevant than the usual idea of equilibrium, employed in single-stock assessments; given the catastrophic impact of many intensive and uncontrolled industrial fisheries (Caddy, MS a)

Analysis of catch and effort data. The simplest and most general approach to assessment of stocks of fish or other species is by analysis of commercially available catch use effort data, leading to the use of production models. From these, estimates of long-term sustainable yield may be obtained and used directly in management of the fishery. This approach is valid and available for cephalopods also and has been applied, for example, in the trawl fishery for cephalopods in West Africa, where initially little information on growth and mortality was available.

Estimation of sustainable yield and optimal effort levels for cephalopods. Monitoring the evolution of catch and effort for trawl fisheries off the western Sahara has witnessed development of trawl fisheries with high initial catch rates followed by declines in catch rates to significantly lower levels, before a new resource attracted the effort. We have already described briefly the decline of sparid stocks in this area, which overlapped in time with growth of the present cephalopod fisheries in the sixties. To date, the decline in catch rates from virgin stock condition has been most extreme for the squid, followed by cuttlefish and then octopus. In a sense, a reverse order of decline would have been expected, since one would tend to expect optimal fishing rates to increase inversely with average longevity; and from what little we know, *Octopus* (2-4 years) appears to survive longer than *Sepia* (2 years) or squid (1-2 years). This would suggest that the relevant factors determining vulnerability to fishing are tied more to availability of the resource to fishing effort and to stock recruitment considerations than just to yield per recruit considerations. Further work on these points seems indicated.

The main problems faced in applying production modelling to the western Sahara trawl fisheries where complete statistics are not available, are well illustrated in extreme form by the *Octopus* fishery. Here as a consequence of the mobility of the several distant water fleets involved, both in terms of grounds and target species involved, and their replacement of each other on the different grounds, it has been difficult to arrive at a common unit of fishing effort. Although relative efforts of different fleets on the same ground can be expressed as the ratio of catches in a given year, this faces problems in incompleteness of catch statistics, in identifying the proportion fished on different grounds, and adjusting this for the changes in fishing power that undoubtedly occurred. Further work has also revealed that *Octopus* on different grounds must be treated as separate stocks, which again has posed problems for the CECAF Working Group for Evaluation of Cephalopod Stocks (FAO 1978, 1982) in establishing separate data series. The rather large charges in total effort exerted, indicate that for some stocks the fishing intensity has greatly exceeded F_{MSY} for a number of years. Despite this, the catch rate has recovered subsequently indicating unlike the sparids, a certain degree of resistance to the effects of overfishing.

Although production modelling has considerable attraction in being theoretically simple because it treats the biological system as a 'black box', it will provide no information that will assist in predicting what is likely to happen in the current season. This is a major disadvantage, since in the case of species liable to major year-to-year fluctuations in abundance, the 'target' yield, whether MSY = Maximum Sustainable Yield, (or better 2/3MSY;close to MEY = Maximum Economic Yield) suggested by the production model will not be constant from year to year, but will be strictly dependent on annual recruitment. This has serious management implications discussed later, but is the main reason for considering in more detail the biological parameters of the species and its ecological interactions.

Mortality Estimation

The ability to estimate potential production for a given cohort and define optimal harvesting strategy with different rates of fishing depends on having reliable estimates of mortality, particularly that due to natural causes, M.

The simplest approach is that by Au (1975) who used the fundamental definition: $M = \bar{t}^{-1}$ to estimate that for a mean life-span of less than one year, M for *Illex* should be of the order of 1.00-1.50. This approach is a useful starting point for assessments, but a number of factors may make this a considerable simplification of the true situation. Predation and cannibalism, being especially focused on the younger individuals, will mean that their M values are correspondingly higher (natural mortality due to cannibalism alone may reach as high as instantaneous values of M = 0.6 over a two-week period for *Illex* (Mohn, 1981)). Contrariwise, we may suspect that since there is a catastrophic post-spawning mortality especially for females, the effective pre-spawning natural death rate for adults may be at or below 1.00-1.50, since this range of estimates is based on the assumption of a steady exponential mortality rate prevailing throughout life. Mohn (1981) uses two approaches for estimating natural mortality rate from cannibalism based on estimated feeding rate and food conversion efficiency, respectively, and shows how environmental variation and food availability may be expected to affect M.

The most usual direct methods of estimation of mortality rates are based on a fished population, and hence provide estimates of total mortality Z. Here the analogous equation to that given above is $X = (\bar{t} - t_c)^{-1}$, where t_c is the mean age at entering the fishery. As noted for *Illex* by Caddy (1979), since many cephalopods are exploited during a limited period of full availability in the course of an essentially migratory life history, estimates of Z must be examined carefully to ensure that immigration or immigration rates are not affecting the overall estimate of mortality, or affecting the estimates of fishing mortality rate F obtained from cohort analysis of weekly catches taken during the fishing season. To some extent, plotting Z estimates against fishing effort should also show up changes in availability. Alternatively, plotting log catch rates against time should show up periods of constant availability as straight line components, possibly permitting the cautious use of Leslie-Delury methods of estimation (see Ricker, 1975) which depend upon a 'closed' population where fishing is the main cause of mortality.

Care must also be exercised in the above that the group of individuals being fished during the season remains the same, i.e., that two or more sequential cohorts from separate spawnings are not confused. Hence, modal analysis of size frequency data should help to avoid obvious errors of this kind.

In a fished population, assuming the above effects can be excluded, the overall mortality rate can be obtained from the catch rates (CPUE) before and after time interval:

$$t_2 - t_1,\ \text{i.e.,}\ Z = \frac{(CPUE_2)\ (CPUE_1)}{t_2 - t_1}$$

An interesting variant of this method was used by Sanders (1979) whereby male and female natural mortality rates are assumed to be the same before spawning, but diverge during the post-spawning period because of greater death rates of females. A joint estimate of pre-spawning M is obtained from plots of Z against effort for a series of years, and the post-spawning values of M by sex can then be obtained approximately by trial and error in a simple simulation to see which values best fit the observed sequence of catches by sex.

Recruitment

Estimation of recruitment in a short-lived species is a key piece of information needed for management of the resource, especially for annual species like squid, where the 'buffering' of changes in biomass from year to year possible for multi-age stocks does not apply, and where the response to environmental conditions is well marked. Looking at similarly short-lived penaeid shrimp populations, Morgan and Garcia (1981) suggested several approaches to estimating recruitment in fisheries for annual species, in addition to the more obvious techniques of larval and juvenile surveys or quantitative estimation of stomach content of predators for abundance of juveniles (Osako and Murata, this publication). The more relevant of these are:

(a) If effort (and q) are reasonably constant, the annual catches are a direct index of R, and
(b) The catch rate at the start of the season may be a good index of the potential yield for the rest of the season, if recruitment occurs during a fairly constant period of the year (e.g., Osako and Murata, this publication for *Todarodes pacificus*, and Sanders (1981) for *Sepia pharaonis*).

Problems in recruitment prediction may however be complicated for some cephalopods, especially where recruitment typically occurs over a prolonged period, or where there are several 'substocks' recruiting at different times of year, as is likely to be the case for tropical and subtropical stocks. Genetic separation is not a necessary prerequisite for occurrence of these subgroups however. Mesnil (1976) suggests that a crossover between spring and autumn spawning with a typical life-span of from roughly 14 to 18 months occurs for *Loligo pealei*. Although the existence of two cohorts out of phase with each other is implied by the above study, there is no reason why at least a limited interchange between them cannot occur: in fact, it seems a reasonable working hypothesis in managing such 'multiple' stocks or stocklets that some such exchange occurs; otherwise, it would be difficult to conceive how this diversification originated in the first place. However, we have as yet no direct evidence that this exchange does occur. Similar or even more complex mechanisms seem implied for other annual species where multiple spawning periods have been documented, and the adaptive value of this intraspecific diversification cannot be doubted from reports of mass mortalities of cephalopods in many parts of the world when unfavourable or extreme environmental conditions may have effectively eliminated one group from the spawning population.

Identification, where possible, of these population subcomponents is obviously important for planning any intensive exploitation of the resource, and where possible also exploitation should be controlled seasonally to avoid extinction of stock subcomponents which must have an adaptive value which is not as yet entirely clear to us.

Stock Assessment Methodology for Short-Lived Migratory Species

It is clear from the foregoing that some care must be exercised before indiscriminately applying standard stock assessment models to these species, although as noted by Sato and Hatanaka (this publication), in absence of reliable biological data, direct estimation of standing stock size by fishing surveys with randomized sampling of the resource is one of the best approaches (the 'Area Swept' method), especially early on in the development of the fishery. Combined with the collection of commercial statistics on total catch and fishing effort, this should provide a useful preliminary basis for management.

In fact, there appear to be at least four basic points to bear in mind in designing a research programme in support of management of cephalopod resources. In addition to proper estimation of total catch and effort, these should be:

(a) Size frequency sampling of the commercial catch at regular intervals throughout the season to allow any different size groups to be distinguished and followed separately as they move through the fishery (using, for example, the methods of modal analysis of e.g., Cassie, 1954, and Bhattacharya, 1967; or Pauly and David, 1980). This sampling scheme should be properly designed so that these groups, after modal separation, can be adjusted up to calculate the actual number they contribute to the total catch in each short interval. This will permit cohort analysis to determine mortality rates for each group;
(b) An understanding of fishery and ecological interactions between cephalopods and other components of the system may have considerable value;
(c) A knowledge of the effects of environmental factors on recruitment variability may eventually be helpful in forecasting of annual returns in an otherwise fluctuating resource, and
(d) Simple simulations of the fishery on a short-time scale (within season) basis (e.g., Hurley and Mohn, 1979; Caddy, 1979) which take the migratory phase into account, will help to define more clearly what is happening on a close to real-time basis by comparison with regular sampling. Some interesting features of these (effectively yield per recruit) simulations are that:

- the mesh size used in a trawl fishery for annual species effectively determines the timing of onset of the fishery, and
- the management criterion of ensuring a 'safe' level of population for an annual species in order to reproduce the next season's stock can be translated into ensuring that an adequate number of survivors reach the onset of emigration, if this coincides with reduced availability to fishing. After this point, since emigration is likely to remove individuals at a greater rate than fishing, exploitation cannot completely decimate the stock.

A totally different modelling approach was adopted by Mohn (1981) that may eventually prove most appropriate given the life history features described earlier. This uses a knowledge of the trophic requirements, conversion efficiency and temperature-related growth in modelling the population, taking into account the occurrence of cannibalism. Although this type of model remains to be tested as a management tool, some of the conclusions (for *Illex*) are interesting:

- cannibalism dominates (by over 60 percent) the total mortality, and increases with bottom temperature; this is partly borne out by faster rates of in-season population decline in warmer years, and evidence of shortage of other food from the high proportion of empty stomachs later in the season, and
- less damage to the population occurs ton for ton from squid captured by early season fishing than later on, since many early season individuals do not survive natural death and cannibalism later on, and in fact their removal may increase the average growth rate, and reduce the possiblity of such food limited processes occurring.

This last conclusion seems to argue against the first conclusion above from simple age-structured models, namely against the use of larger mesh size (and later onset) of the fishery. Remember however that trawl fisheries are usually mixed species fisheries, and it may be necessary to consider the impact of low mesh sizes on other species in the catch.

Mesh Selectivity

Although there appears to be little evidence of significant selectivity for various sizes of jigs (Ehrhardt *et al.*, this publication), a limited amount of work has been performed on mesh selectivity of trawls for *Octopus* (Guerra, summarized in CECAF, 1979), for *Illex* (Clay, 1979), and for *Sepia* (Sanders, this publication). Rather irregular selectivity curves are often observed, and it would seem that considerable variation in selectivity is caused by the fact that the tentacles can impede elimination of small individuals on the one hand, and the extreme body plasticity of squid and octopus can assist large individuals to escape, on the other hand. However, typical selection factors for *Illex* were in the range:

$$\text{Selection factor} = \frac{\text{mantle length (mm)}}{\text{codend stretched mesh size (mm)}} = 2.00\text{-}2.60 \text{ for } 60\text{-}120 \text{ mm mesh sizes}$$

Having a more rigid body form, *Sepia* may be expected to show a more regular selection pattern (Sanders, this publication).

An alternate approach to formal gear selection studies, is the analysis of the effects of mesh selection on yield by cohort analysis using size frequency data (Jones, 1981) and this seems well worth considering here, at least to determine mortality rate at size under various assumptions on growth and natural mortality.

Rarely, however, is the selectivity of a given year for a single target species the only important consideration, as may be illustrated by the following example for a multi-species cephalopod fishery where a mixture of species occurs in the catch.

Mesh Size Regulation in the Western Sahara Trawl Fishery

Concern over the appropriate mesh size to use in the trawl fisheries off the western Sahara has been regularly expressed by FAO fisheries working groups since the early seventies even before cephalopods became the dominant catch component. In 1972, it was recommended that mesh sizes below 60 mm be barred in cephalopod fisheries in order to facilitate adoption of a 70 mm mesh in hake and sparid fisheries, since this would reduce discarding and consequent mortality of small sparids in the cephalopod fishery. Most trawl fisheries in the area are now reported to be using 60-70 mm mesh, although the selectivity of 70 mm and larger mesh in the cephalopod fisheries does not yet seem to have been rigorously tested, either in terms of its direct impact on cephalopod yield, or in terms of its impact on discarding practices with regard to other species. Given the intensive nature of this fishery on cephalopod grounds (fishing mortality rates of F = 1.0 - 1.5 have been estimated, roughly equivalent to 63-78 percent of the stock removed each year), the occurrence of a significant discard rate, particularly for juveniles of other key fish species (especially sparids) in the cephalopod fishery will certainly have an adverse effect on their later recruitment to other fisheries, and in fact, may be one of those factors hindering recovery of formerly abundant fish resources. Further study of these fisheries interactions is needed at all stages of the life history.

It may be worth briefly looking here at cephalopod fisheries in other areas of the world, e.g., the squid (*Illex illecebrosus*) fishery in the northwest Atlantic, where more detailed analyses have been carried out, and where small mesh fisheries (60 mm) for squid and silver hake have been directly implicated in adversely affecting recruitment to other important groundfish species in the area (ICNAF Assessment Sub-Committee Report, 1979).

After comparative trawling experiments in the northwest Atlantic, it was demonstrated for this relatively small species of squid (600-800 g maximum weight) that a change from 60 to 90 mm mesh size in the codend would result in no short-term or long-term drop in yield for squid, but would simply postpone the time that each cohort entered the fishery by several months (Figure 7), as well as reducing the discard rate on small hake. Incidentally, the optimal rate of fishing that the squid stock could sustain without decline in economic yield would probably be increased by this measure. The implications of this elsewhere must be considered with caution, but it illustrates three main points:

(a) Larger mesh size than currently in effect may well prove to be desirable for its direct effects in increasing yield.
(b) A correct evaluation of optimal mesh size should take into account not only increased yield of the target species, but also its impact on other commercially important species in the ecosystem.
(c) An increase in mesh size for annual species effectively acts to postpone onset of the fishery.

One may suppose however that in general, mesh size regulation, though desirable, may be secondary in importance to effort limitation with respect to increasing yield. For example, at present effort levels in the Saharan fishery with the 60 mm mesh size now in effect, it is calculated that spawning potential of octopus is reduced to 10 percent of the unexploited stock fecundity (Pereiro and Bravo de Laguna, 1979).

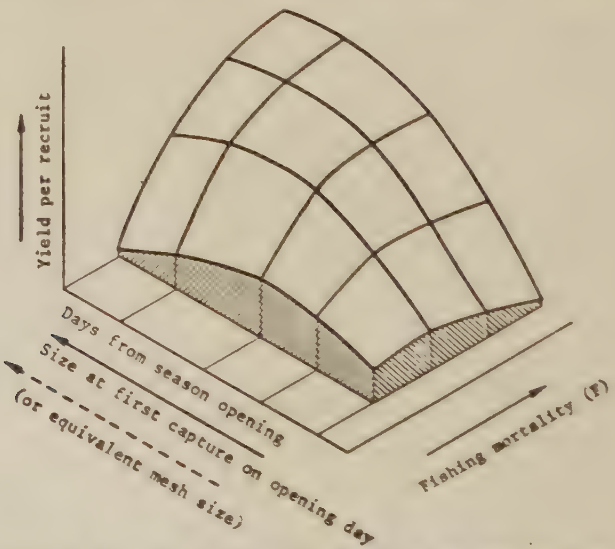


Figure 7 Response surface showing effects of fishing mortality and changes in size at first capture (or date of opening of the fishery) on the yield per recruit for *Illex* (Hurley and Mohn, 1979)

Area-Swept Assessments

This method of utilizing catch data from properly planned, stratified random research surveys, provides population estimates even in absence of detailed biological information. As noted by Sissenwine (1976), if a trawl efficiency of unity is assumed, this method will underestimate the size of the resource so that if (say) the 40 percent annual exploitation rate rather arbitrarily adopted by ICNAF is used in setting TACs, the chances of serious overfishing are reduced.

We may note that prior to such surveys, it is assumed that the survey area (designed to include the boundaries of the stock distribution) is divided into strata on the basis of preliminary information as to whether the cephalopods are likely to be abundant, common or infrequent in each part of the subarea: frequency of stations samples being kept roughly in proportion to expected abundance in order to improve the efficiency of the survey and its statistical precision. Then, paraphrasing Mesnil (1977), if n_i stations are then fished in each stratum i of total area A_i, and b_i is the area swept per stratum (= b x n_i, if a standard area b is swept by the gear), and Y_i is the total catch (weight or number) per stratum:

Stock size (B_i) per stratum is then:

$$B_i = \frac{A_i}{b_i} \times Y_i \quad \text{or} \quad B_i = \frac{A_i}{b} \times \frac{Y_i}{n_i}$$

and total stock size $B_T = \text{Sum}_i (B_i)$

If s_i is now the variance between the n_i tows in the ith stratum, the variance of B_T is then given by:

$$S_B^2 = \text{Sum}_i \left[\frac{A_i^2 \times n_i \times S_i^2}{b_i^2} \right]$$

The standard error of this estimate is then S_B.

Tagging

This method is theoretically practical for following migrations of cephalopods (if adequate coverage exists by fisheries to give a chance of tag recovery), and has been used both in North America and by Japan. It poses significant practical and theoretical problems however, because of the fragile body, highly active behaviour and short life-span and likelihood of significant tag loss due to the self-cleaning behaviour and well-structured dominance shown within squid schools (O'Dor *et al.*, 1979). It must be concluded that this method should only be secondary to detailed analysis of size structure of the catch and area-swept methods. Reference is however, made to Jones (1976) for methods of analysing tag return data and to Garcia and Le Reste (1981), who also give a detailed review of methods of stock assessment for penaeid shrimp, which may have wider application for other short-lived species.

MANAGEMENT OF CEPHALOPOD STOCKS

Short and Long-Term Management Measures

A practical distinction can be made in management of marine resources between the kind of management decisions that once made and implemented can, allowing for periodic review and adjustment, be left in place (if compliance by the industry of government enforcement of regulations can be assured), and those regulations which must be adjusted on an annual or even semi-annual basis. This distinction is particularly relevant for short-lived species, such as cephalopods, and is helpful in deciding on management priorities.

The general principle should be that unless management mechanisms are well-developed, major emphasis should be placed on those kinds of decisions that once made, do not need major readjustments to offer significant benefits, rather than short-term mechanisms that require frequent, informed decisions to be successful, although in practice, a combination of both, plus a regular surveillance of this impact will be needed.

Some examples of these two types of measures are:

A. Long-term measures

(i) Mesh size regulations/size limits/discard regulations
(ii) Pre-arranged and constant seasonal or area closures (e.g., a known spawning ground closed during a known spawning season)
(iii) An overall limit to the tonnage or combined hp of the fleet that will avoid overfishing in 'poor' years

B. Short-term measures

(iv) Supplementary to (iii) (as a 'fine adjustment' mechanism), an additional number of boats of known fishing power may be given temporary licences to fish within a given area in each year
(v) An overall quota and allocation of the total catch may be made annually by vessel class, country, or gear type, by year or season
(vi) Variable timing of resource harvesting onset or termination (depending on, e.g., a minimum catch rate or minimum spawning biomass being reached, or on the occurrence of some biological event, e.g., a catastrophic poor-spawning mortality or emigration from the fishing grounds)

Description of Individual Measures

The first category of measures has obvious advantages in terms of the framing of regulations, since these can be accomplished with a reasonable lead time and, if effective, can be left in place. A review of some of these management measures is given in Caddy MS (b).

(i) Mesh size regulation in the western Sahara trawl fishery has been discussed extensively for the groundfish species forming the major components of the trawl fishery, but less so for the cephalopods, and relatively few experimental selectivity studies have been carried out to date on these species. With respect to groundfish, optimum mesh sizes as high as 90/100 mm (sparids) have been suggested for individual species (FAO, 1971), and an overall minimum mesh size of 70 mm has been suggested for groundfish (FAO, 1970). Mesh size studies on cephalopods are even more sparse, and although it has been demonstrated in a preliminary way that an increase in mesh size from 40 to 60 mm will probably be beneficial for *Octopus* (CECAF, 1979), we know little or nothing with respect to the effects of further increases in mesh size, or the optima for squids or cuttlefish. It seems likely however, from more extensive studies carried out in other areas (Clay, 1979), that a minimum of not less than 70 mm will prove to be the case for other fairly large cephalopods also.

A few generalizations may be useful with respect to mesh selection of cephalopods: by their morphology, most cephalopods are very elastic in shape, with tangling tentacles, which often makes the 50 percent selection point difficult to measure. The size range over which partial retention occurs usually occupies a significant fraction of the total growth stanza for the species. In addition, we may note that for short-lived (annual) species, the mesh size in use determines not only the size at first capture, but the date of onset of the fishery (Hurley and Mohn, 1979) (Figure 7). Mesh size can therefore be used as an indirect way of controlling onset of the fishery, especially for squids. Also, studies on *Illex illecebrosus* show that a mesh size as high as 90 mm would be unlikely to have an adverse effect on overall yield, although it would postpone the fishery until most squid had reached at least 20 cm mantle length (Clay, 1979).

(ii) Seasonal/area closures are much more controversial measures, although if there is an interest in recovery or maintenance of stocks of those sparids and of *Sepia* that form spawning aggregations in shallow waters and hence are vulnerable to fishing at this time, such measures as a seasonal closure for trawling or other highly efficient methods of capture may be useful temporary means of allowing stock recovery. Further study and definition of the localized spawning areas and the time of year and areas where these aggregations occur will be needed however.

(iii) Effort limitation: If it is decided that regulation is to be by means of effort control as opposed to quotas, a rough limit on the total amount of effort allowed to be exerted annually in the fishery can be achieved by controlling the fleet size, after allowing for differences and changes in fishing power. This may be regarded as a 'coarse tuning' of the system, which it may or may not be decided to supplement by means of short-term measures, such as a limit on the number of days fished (closed seasons). Using this approach, and aiming at some optimum, physical or economic objective (e.g., MEY, $F_{0.1}$) we can exert some control on both the abundance of the main species sought, their size range, and possibly even the species composition. For example, if we consider in the case of the western Sahara trawl fishery, that the original sparid-dominated community is analogous to a 'climax' ecosystem in terrestrial terms it is possible (although by no means certain) that a low fishing intensity on sparids could lead to a reversal of the cephalopod dominance, while a continued increase in fishing intensity may lead to other changes in the dominant species (now octopus) which may not necessarily be as favourable for human harvesting (comparable, for example, to the 'bloom' of *Balistes*, fish species of low commercial value which has recently dominated in the trawl fisheries of the southern CECAF area).

(iv) Quotas: The setting of quotas for cephalopod management poses serious practical problems even when the necessary assessment management and enforcement mechanisms are set up, which is not yet the case in all parts of the world. Even in the event that a predictive mechanism can be found to ensure that a minimum biomass or optimal spawning stock is left at the end of the seasonal fishery, the rapidity with which this kind of assessment must be carried out, the results analysed, compared with prevailing fishing patterns, and discussed with the management authorities concerned, poses formidable problems even before implementation begins. A comparison of effort control measures with quota management is provided in Table 1.

Some of the reasons that suggest that some form of effort control is the most feasible approach for cephalopods are given in Table 1, which summarizes the relative merits and disadvantages of this type of approach compared with quota control for short-lived species.

(v) Variable timing of a fishery: As with quota control, this depends on real-time monitoring of statistics, in this case the catch rate, based on the Leslie-DeLury type of models: that is, the yield to be expected from a fishery in a given year might under certain circumstances be predictable from the catch rate early in the season, as noted by Sanders (1979) for the Red Sea *Sepia pharaonis* fishery.

ONE APPROACH TO EFFORT LIMITATION FOR SHORT-LIVED SPECIES

The following section concentrates on outlining the kind of machinery that must underline successful effort control in short-lived species. It is clear from experience elsewhere that 'limited entry' will not be wholly successful if it simply relies on fixing the number of boats or days on ground in the first year of management and then neglecting further adjustments to the fishery in future years. Both adequate and continuing machinery for collecting and analysing information on the state of the resources, as well as decision-making mechanisms for closely coordinating resource monitoring with licensing and enforcement are needed, either at a national or at a sub-regional level. An example of such a

Table 1

Comparison of effort limitation and quota control for cephalopod fisheries

Effort control	Quota control
Advantages	Advantages
1. This measure is not so dependent on real-time information on total catch as is quota control (i.e., the number and impact of short-term decisions is reduced).	1. Superficially, quota control allows for better economic planning in the production and marketing sectors at least one year in advance of the main period of production.
2. From the point of view of enforcement, reducing the need for real-time monitoring of the catch of all vessels on a daily or weekly basis (necessary for quota control) is a major saving in patrol vessel and enforcement service time. Patrol vessels can now concentrate their efforts largely on: (a) ensuring that only accredited boats are in the zone, and that other fisheries regulations are enforced; (b) by occasional spot checks on accredited fishing vessels patrol vessels can establish that they are catching only those species for which they are licensed to fish, and are observing any other regulations on mesh size or discards that may be in effect.	2. In the case of multi-age group fisheries where the stock size of post-recruits can be roughly predicted in advance of onset of the fishery (this presupposes good statistics, and an extensive research input), setting of a quota which can be monitored and enforced, allows the state of the stock at the end of the season to be known with varying degrees of reliability, as long as the newly recruited year class is not a major component of the yield.
3. Although observations at sea are desirable in order to monitor changes in fishing practice that may affect fishing power of the vessels participating, these can be occasional, and incidental to any biological sampling of the catch that is essential to the monitoring scheme.	3. Allocation schemes between different components of the fishery can be decided in advance of the fishery.
4. If some independent method is used to follow changes in the fishing power or fishing intensity of the fleet (which will occur slowly, even if fleet size is kept constant), this method ensures that any pre-set rate of harvesting is not greatly exceeded at least in the short term, irrespective of any changes in abundance that may occur.	
5. This method is independent of an exact knowledge of stock size, in that harvesting at close to the f_{opt} level will occur independently of stock sizes if fishing effort is properly adjusted.	
6. A two-tier system of licensing can be used if resources are very variable, involving a minimum of permanently licensed boats, and temporary licences to harvest temporary high abundance levels.	

Table 1 (continued)

Effort control	Quota control
Disadvantages	Disadvantages
1. Long-range economic planning by those participating in the fishery is made difficult, at least with respect to future annual yield. However, the risks of wrong decisions on licensing are largely transferred to the vessel owners. (Note that if recruitment is irregular, long-range planning is not possible even with quota control).	1. For short-lived species we cannot yet predict recruitment size, and hence set an annual quota which will not exceed the sustainable yield a year in advance of the fishery. As a result there is: (a) a high risk of serious overfishing of cephalopods and associated species exists (up to several times optimal removals with an arbitrary quota based on, e.g., the last year's catch), if a temporary decline in year class size causes abundance to fall significantly below average levels for previous years; (b) with a very cautious fishing regime, there is a significant chance of underutilizing the resource.
2. Unless there is an independent monitoring of the fishery and collection of basic data from which fishing intensity can be calculated, unregistered increases in fishing power can result in long-term changes in exploitation rate, even if fleet size stays constant, due to learning factors, as well as improvements in gear design and deployment. However, these changes are unlikely to much exceed 10 percent per year. Keeping up with these changes requires occasional monitoring of the fleet (rather than quota control where monitoring of all landings from the stock is necessary).	2. Theoretically at least, research vessel surveys can be carried out before the opening of the season to establish biomass levels present, and hence help in setting national quotas. In fact, due to the inevitable delays between completion of the cruise, analysis of the data, and convening of the management authority, there will be insufficient time to implement quota decisions before opening of the fishery, especially if recruitment is more than once annually. If recruitment occurs more than once annually more than one control-point (and hence semi-annual quotas) will be needed. This is impractical, but setting of quotas in absence of data on stock size recruited will eventually lead to stock depletion in poor recruitment years.
3. Manipulation and allocation of the number of licences may pose few problems to the coastal state with respect to the foreign fleet, but significant political problems with respect to the domestic fleet.	3. If a mixture of species occur in the fishery, all or many of which are susceptible to overfishing and need management, individual quota control soon becomes impractical. An overall quota on all species offers little or no advantage over effort control, does not prevent overexploitation, and has a negligible scientific basis.
	4. Administrative capabilities may not be sufficient at the start of the EEZ era to ensure collection of comprehensive and reliable catch statistics.
	5. Major incentives (and opportunities) exist to misreport catches unless there is a major investment in surveillance.
	6. If the quota is on distant water fleets, inspection needs may dictate local landing and transhipment of the product. This imposes the need for good port and storage facilities on shore.

coordinated management structure and its operation sequence is given in Table 2. The approach outlined below sacrifices precision in deciding on the level of catch to be aimed for in the next management period (a precision which is often likely to be spurious anyway), for a more empirical approach that takes into account recent and historical catch levels and all available biological data, and attempts to regulate the intensity of harvesting directly. Permission to participate in the fishery is reserved for a limited number of vessels with known characteristics, whose fishing success is otherwise governed by the abundance of the resource. The fleet is only monitored to the extent necessary to ensure compliance with the conditions of the fishing licence, and to collect the necessary statistical data in order to provide the required input for decisions on licensing in subsequent management periods.

The basic premise of management as stated above, is to ensure as closely as possible, that the exploitation rate should not exceed some upper limit above which future recruitment may be affected. A harvesting rate of 40 percent of the existing stock annually is suggested as a reasonable objective in line with practice elsewhere, although this should be modified by local experience, particularly if this rate of harvesting is shown to be seriously affecting by-catch species taken incidentally in the same area as the cephalopod fisheries.

If it is felt that the degree of uncertainty with respect to the returns from fishing in a given season discourage the payment of a significant licence fee for access to the resource, or alternatively, if the returns to the management authority from the licence fee are not commensurate with potential landings in a good year, then the agreement to fish can include provisions for additional payment, related to level of catch such as, for example, a tax on landings1/. Such an approach would, of course, be more costly than simple effort control in that, as for quota control, knowledge of the true catch becomes essential, necessitating on-vessel observers or other monitoring mechanisms. Whatever economic objectives and mechanisms are decided on (and this paper is not specifically concerned with these points), it is basic to the scheme of effort control that fleet size and, more specifically, harvesting rates, do not seriously exceed some pre-set level, corresponding to (say) 40 percent stock removals annually.

SUMMARY OF IMPLICATIONS FOR MANAGEMENT OF CEPHALOPOD FISHERIES

Three situations seem to occur in looking at the needs for research and management of cephalopod stocks:

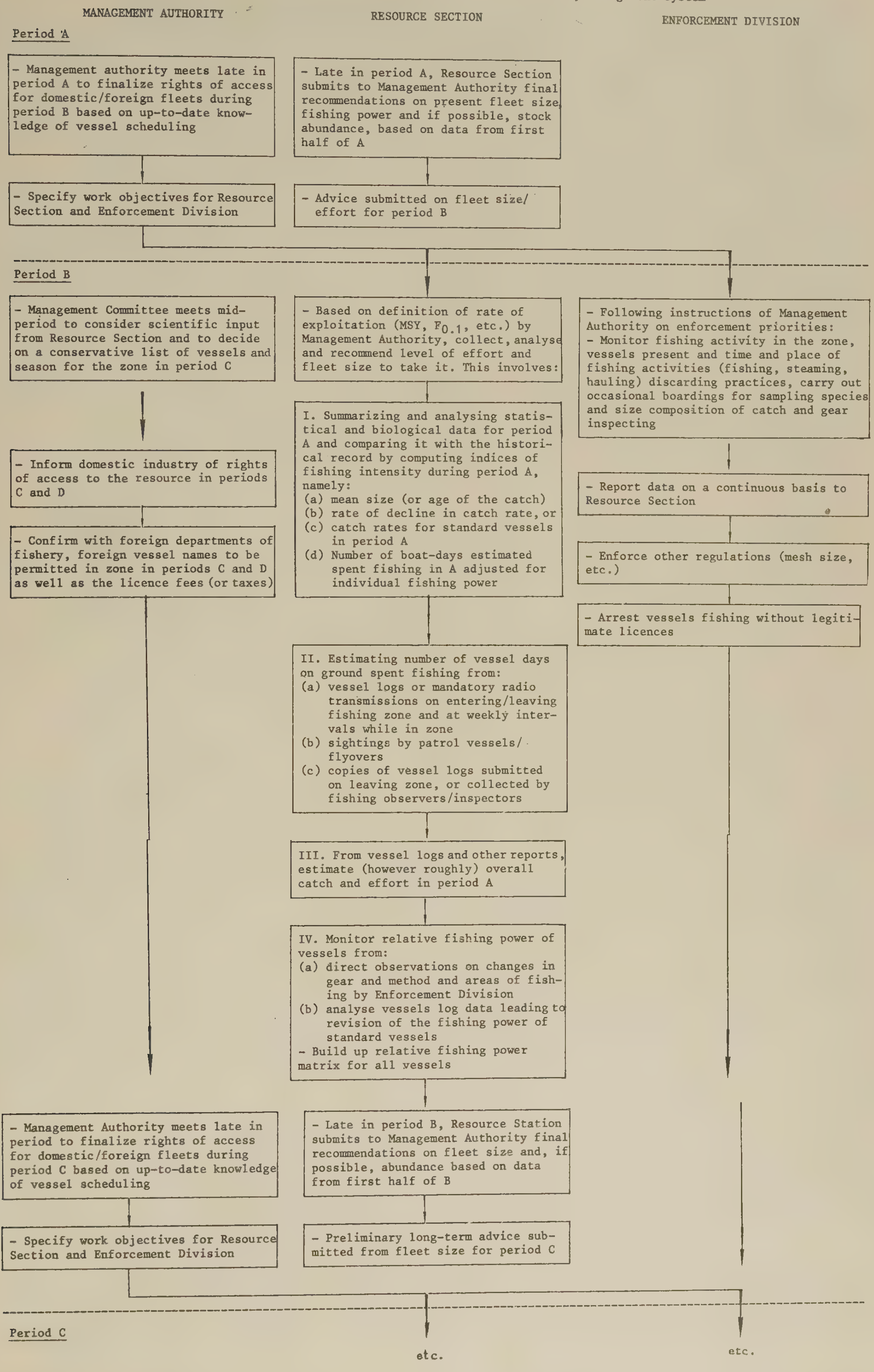
(a) If cephalopods form a small incidental part of the catch for other species, they may be given a relatively low priority in research, but a higher priority in exploratory fishing with various types of gear, such as those used by the Japanese fishery (see Osako and Murata, this publication). Some brief examination of stomach contents of predatory fish in the area early on in the resource investigation programme might

---

1/ Such a landing tax has been considered a self-sufficient management measure of itself in absence of other measures, in that increase in effort will in the long term decrease catch rates, and hence profitability of the fishery, to the point that, after tax, there exists no incentive to expend further effort. In the short term however, this can lead to serious overfishing if abundance is low and demand high; and should only be regarded as a 'coarse tuning' of the system. Biological sampling, effort management and enforcement will still be necessary if maximizing yield (or just preventing stock depletion) are management objectives, even if only to decide on the appropriate level of taxation in light of fluctuating market prices for fuel and fish. Limited entry plus monitoring of the fleet and the stock size to ensure the latter does not drop below a pre-set minimum will still be necessary, since otherwise in any one year an excessive number of vessels may continue to fish at 'subeconomic' levels if access to other fisheries is restricted, or if they need to fulfil pre-set production targets.

Table 2

Functions and interrelations of the three components of a fishery management system



MANAGEMENT AUTHORITY

RESOURCE SECTION

ENFORCEMENT DIVISION

Period A

MANAGEMENT AUTHORITY:

- Management authority meets late in period A to finalize rights of access for domestic/foreign fleets during period B based on up-to-date knowledge of vessel scheduling
- Specify work objectives for Resource Section and Enforcement Division

RESOURCE SECTION:

- Late in period A, Resource Section submits to Management Authority final recommendations on present fleet size, fishing power and if possible, stock abundance, based on data from first half of A
- Advice submitted on fleet size/effort for period B

Period B

MANAGEMENT AUTHORITY:

- Management Committee meets mid-period to consider scientific input from Resource Section and to decide on a conservative list of vessels and season for the zone in period C
- Inform domestic industry of rights of access to the resource in periods C and D
- Confirm with foreign departments of fishery, foreign vessel names to be permitted in zone in periods C and D as well as the licence fees (or taxes)

RESOURCE SECTION:

- Based on definition of rate of exploitation (MSY, $F_{0.1}$, etc.) by Management Authority, collect, analyse and recommend level of effort and fleet size to take it. This involves:

I. Summarizing and analysing statistical and biological data for period A and comparing it with the historical record by computing indices of fishing intensity during period A, namely:
(a) mean size (or age of the catch)
(b) rate of decline in catch rate, or
(c) catch rates for standard vessels in period A
(d) Number of boat-days estimated spent fishing in A adjusted for individual fishing power

II. Estimating number of vessel days on ground spent fishing from:
(a) vessel logs or mandatory radio transmissions on entering/leaving fishing zone and at weekly intervals while in zone
(b) sightings by patrol vessels/flyovers
(c) copies of vessel logs submitted on leaving zone, or collected by fishing observers/inspectors

III. From vessel logs and other reports, estimate (however roughly) overall catch and effort in period A

IV. Monitor relative fishing power of vessels from:
(a) direct observations on changes in gear and method and areas of fishing by Enforcement Division
(b) analyse vessels log data leading to revision of the fishing power of standard vessels
- Build up relative fishing power matrix for all vessels

ENFORCEMENT DIVISION:

- Following instructions of Management Authority on enforcement priorities:
- Monitor fishing activity in the zone, vessels present and time and place of fishing activities (fishing, steaming, hauling) discarding practices, carry out occasional boardings for sampling species and size composition of catch and gear inspecting
- Report data on a continuous basis to Resource Section
- Enforce other regulations (mesh size, etc.)
- Arrest vessels fishing without legitimate licences

MANAGEMENT AUTHORITY:

- Management Authority meets late in period to finalize rights of access for domestic/foreign fleets during period C based on up-to-date knowledge of vessel scheduling
- Specify work objectives for Resource Section and Enforcement Division

RESOURCE SECTION:

- Late in period B, Resource Station submits to Management Authority final recommendations on fleet size and, if possible, abundance based on data from first half of B
- Preliminary long-term advice submitted from fleet size for period C

Period C

etc.

etc.

give an idea of potentially important ecological interactions. Specific management measures may not be strictly necessary for cephalopods in a mixed fishery since their stocks are likely to be more resilient to fishing than most of the target fish species. Therefore, in this case, investigation of the cephalopod resource may need to achieve no more than is consistent with having a reasonable knowledge of the main fishery components, unless a large expansion of this fishery is foreseen. Catch data should however be collected by species, and a series of effort data common to both cephalopods and the other main components of the resource should be collected;

(b) Assuming that a mixed trawl fishery develops at moderate levels of exploitation with a cephalopod species as the main target, the problems mentioned earlier of mixed species management arise, namely, deciding on a common mesh size and fishing intensity. Unless the groundfish or pelagic fish species is an unimportant part of the by-catch, deciding on yield-pre-recruit optima for fishing intensity and size at first capture for cephalopods alone, will likely result in conditions of exploitation unfavourable to other, often multi-age class species. If this seems confirmed, the use of selective harvesting methods for cephalopods should be encouraged. In any case, in addition to the total yield and catch rate data needed for basic fisheries management, other data bases and management measures should be considered. First of these should be routine collection of sample data on size composition of the catch, permitting modal analysis and determination of the growth rate, and estimation of mortality rates by means of length-specific cohort analysis. The institution of routine at-sea surveys to determine stock size, especially early on in the period of availability of the cohort will allow some idea of stock size of cephalopods, and (after several years of data have accumulated) also give an index of possible catch throughout the course of the season. This kind of data could theoretically be used for setting catch quotas, but in view of the short life-span of these species and the considerable manpower and costs associated with real-time fishery management, effort regulation appears to offer a more sensible approach to management. In this case, management could be based on a simultaneous monitoring of fleet size, fishing power and time on the ground, combined with direct estimation of mortality rates from size frequency analysis, thus permitting the allowable fleet size to be adjusted in the following season. One other factor that needs to be considered here is to note that in the case of fisheries dependent on mesh size, the size of mesh for an annual species with a discrete time of recruitment to the grounds effectively determines the timing of onset of the fishery, and

(c) In the case of extremely intensive fisheries using specialized gear, it is still possible for overfishing to occur even for these highly productive resources. This appears to have happened in the case of the *Todarodes* fishery in Japan. For cuttlefish, which often spawn inshore on relatively specific breeding grounds, some additional concern may be necessary to avoid too intensive fishing here during the spawning period. In the case of octopus which is shelter-limited in its habitat, the construction of artificial reefs and shelters is being attempted in Japan to increase potential production. For moderate to intensive cephalopod fisheries, the problem of management becomes not only one of preventing long-term overfishing of the resource, but also of making fisheries forecasts of where and when the best yield can be taken. Here a knowledge of the details of stock spawning and migration becomes necessary, plus the setting up of indices of pre-recruit abundance before the season starts. Since cephalopods are often regarded as r-selected 'epidemic' species, we may expect that large population fluctuations will affect resource harvest potential (Caddy, in press a). To date, our mastery of the application of forecasting methods outside of Japanese waters is rather limited, but presents an essential area for future research.

SUMMARY AND CONCLUSIONS

1. More attention should be paid to an understanding of the biology and population dynamics of this diverse group of organisms, and the first aspect that merits attention from fisheries biologists and managers is an understanding of the important role they play in the marine ecosystem. Cephalopods are a key component in the diets of many fish and marine mammals. Species of octopus and cuttlefish (and to some extent, neritic squid) play a role in the transfer of biomass between the macrobenthos and that of predatory fish, similar to the intermediary role played by the smaller oceanic squid in transferring zooplankton biomass to the larger predators of the oceanic food web (e.g., the toothed whales and some tunas). Their role in the marine ecosystem is more likely to be appreciated from examination of the stomach contents of predators than from catches of

cephalopods in conventional fishing gear, since experience in Japan and elsewhere in the Far East has shown that specialized methods of fishing (e.g., octopus traps, jigging machines and surface gillnets) will usually need to be developed to harvest or monitor these resources effectively. Cephalopods as a group may generally be characterized as opportunistic animals, with high rates of reproduction, population growth and mortality; features which make for a high rate of production relative to their biomass, which again will make biomass estimates from fishery surveys tend to underestimate the importance of cephalopods in marine food webs.

2. In light of the above, the Resource Manager cannot completely disassociate management of cephalopods from that of other key resources of the ecosystem: in fact, there is growing evidence that cephalopod biomass will increase as a result of, e.g., heavy fishing of predators on cephalopods. Such predators would, in the unexploited ecosystem, be the main factors controlling cephalopod abundance. Further, increased predation by larger squid on juvenile stages of many fish species (and by *Octopus* and *Sepia*, on commercially valuable crustacea), although more difficult to document, may in turn be consequences of excessive depletion of stocks of predatory fish. We may therefore suggest that the earliest priority in cephalopod research and management after identification of the main species and stocks, is to monitor and control catch and effort levels aimed at other ecosystem components feeding on cephalopods! There is no suggestion here that with our present state of knowledge, species interactions of this kind apply in all circumstances, or can ever be quantified, but their existence should be borne in mind by the manager.

3. A more direct example of interaction between cephalopod fisheries and those for fish species is provided by the mixed species trawl fishery. Mesh size regulations aimed at the generally smaller cephalopods may result in large numbers of discards of juvenile fish in the by-catch, and since cephalopods are (with certain exceptions) fairly resistant to high fishing pressure, this may eventually have repercussions on the ability of these fish resources to maintain their population size. This is perhaps a good reason for using specialized methods of harvesting cephalopods, namely in order to reduce the unproductive loss of fish by-catch from the mixed fisheries themselves.

4. Cephalopods appear to be highly opportunistic species, capable of rapidly expanding their population size to occupy niches left unoccupied by the depletion of other resources, and because of their opportunistic feeding patterns, are likely to be capable of exerting significant ecological pressure on other components of the ecosystem. Management of these resources will certainly have to be closely coordinated with that for other resources, because of the likelihood of significant species and fishery interactions. To what extent steady yield from these resources will prove sustainable in the long run is uncertain, but it seems likely that significant order-of-magnitude changes in their abundance and recruitment will occur over time. The possibility of further transitions to one or more other dominant species, not necessarily as favourable to commercial utilization, is not precluded, particularly if fishing effort increases still further and results in continued depletion of spawning stocks of the target species.

5. Management of short-lived cephalopod species poses some rather different problems from those associated with multi-aged finfish species. In particular, their short life-span means that unless there is a real-time immediate response to changes in the fishery which is rarely possible in practice, stock depletion will result in a serious impact on recruiting year class size next year if catch quotas are maintained constant. Real-time management, by catch quotas unless set at a low level, or supported by regular seasonal surveys, seems less practical here, especially where two recruitment periods occur in a year. Some variant of effort control seems the only practical alternative for maintaining minimum biomass levels, since it requires relatively small short-term adjustments - principally for changes in fishing power. These are unlikely to exceed 10 percent per year for a given class of vessels, whereas under management with fixed quotas, exploitation rates may vary by several hundred percent, depending on recruitment. As a provisional biological objective, it is suggested that effort levels be adjusted to remove no more than 40 percent of the fishable biomass in any year.

6. Other options that can be easily included under effort control are the taxation of landings from the fishery, or the adjustment of licence fees by some form of auction of

limited rights of access. The former option will of course require more exacting surveillance, but will have the advantage that revenues in a fishery under effort control, where removals are likely to vary considerably from year to year, will reflect the removals without requiring a pre-set TAC to be defined. As with the second option, the economic consequences of poor predictions of stock size will be largely felt by the vessel owners rather than by the management authority, whose main role is to ensure maintenance of the level of resource.

7. Close coordination will be required between the management authority, the resource monitoring service (responsible for monitoring intensity of fishing from statistics and biological sampling), and the enforcement branch. Licence fees sufficient to support these activities should ideally be set aside from revenues generated by the fishery.

8. Another regulation that may be considered if recovery of overfished *Sepia* stocks is a desirable objective, is temporary closure of fishing in the vicinity of spawning grounds when major concentrations of breeding adults are present.

9. Mesh size regulations should, where possible, be made uniform for the entire trawl fishery. The mesh size selected is then that with the most favourable properties for improving yield and reducing discards integrated over all the main trawl fisheries. This seems likely to be at least 70 mm stretched mesh.

REFERENCES

Amaratunga, T., Preliminary estimates of predation by the short-finned squid (*Illex*
1980 *illecebrosus*) on the Scotian Shelf. NAFO SCRS. Doc. 80/II/31, Ser. No. 63

Amaratunga, T., *et al.*, Food and feeding of the short-finned squid, *Illex illecebrosus*,
1979 on the Scotian Shelf in 1978. ICNAF Res. Doc. 79/III/11, Ser. No. 5336:24 p.

Araya, H., Some problems of the conservation for the jigging fishery resources of a
1974 common squid, *Todarodes pacificus*, Steenstrup in Japan. Gyogyo Shigen Kenyu Kaigiho/Rep.Fish.Resour.Invest.Sci.Fish.Agency Jap., (16):71-8. Translated by Multilingual Services Division, Translation Bureau, Department of the Secretary of State, Canada

Au, D., Considerations on squid (*Loligo* and *Illex*) population dynamics and recommenda-
1975 tions for rational exploitation. ICNAF Res. Doc. 75/61, Ser. No. 3543

Beverton, R.J.H. and S.J. Holt, A review of methods for estimating mortality rates in
1956 exploited fish populations, with special reference to sources of bias in catch sampling. Rapp.P.-V.Réun.CIEM, 140:58-66

____________, On the dynamics of exploited fish populations. Fish.Invest.Minist.Agric.
1957 Fish.Food G.B.(2 Sea Fish.), 19:533 p.

Bhattacharya, C.G., A simple method of resolution of a distribution into Gaussian com-
1967 ponents. Biometrics, 23:115-35

Bravo de Laguna, J., *et al.*, Actividad de la flota pesquera española en aguas del banco
1976 Sahariano durante 1975. Inf.Pesq.Inst.Esp.Oceanogr., (6)

Caddy, J.F., Preliminary analysis of mortality, immigration and emigration of *Illex* popu-
1979 lation on the Scotian Shelf. ICNAF Res. Doc. 79/VI/120, Ser. No. 5488:20 p.

____________, Management of shrimp fisheries. *In* Fish by-catch...bonus from the sea.
1982 Report of a Technical Consultation on shrimp by-catch utilization, held in Georgetown, Guyana, 27-30 October 1981, sponsored jointly by FAO and IDRC. Ottawa, IDRC (IDRC-198e):120-3

____________, (a) An alternative to equilibrium theory for management of fisheries. Background paper to FAO Expert Consultation on the regulation of fishery effort (fishing mortality). 17-26 January 1983 - Rome, Italy (MS)

Caddy, J.F., (b) Indirect approaches to regulation of fishing effort. An introductory paper for Session II, Panel II of 2 FAO Expert Consultation on the regulation of fishery effort (fishing mortality). 17-26 January 1983 - Rome, Italy (MS)

Cassie, R.M., Some uses of probability paper in the analysis of size frequency distri-
1954 butions. Aust.J.Mar.Freshwat.Res., 5(3):513-22

Clay, D., Mesh selection of silver hake (*Merluccius bilinearis*) in other trawls on the
1979 Scotian Shelf with reference to selection of squid (*Illex illecebrosus*). ICNAF Res. Doc. 79/II/3:36 p.

Conover, R.J., Transformation of organic matter. *In* Marine ecology: a comprehensive
1978 treatise on life in oceans and coastal waters, edited by O. Kinne. Vol.4. Dynamics. New York, John Wiley and Sons, pp. 221-456

Doi, T. and T. Kawakami, Biomass of Japanese common squid, *Todarodes pacificus*, Steenstrup
1979 and the management of its fishery. Bull.Tokai.Reg.Fish.Res.Lab., (99):65-83 (in Japanese, English summary)

Dong, Z., The present status and the prospects of cephalopod resources in the West
1981 Pacific. Informal partial translation by S. Chikuni from J.Fish.China, 5(3):263-70

Durand, J.R., Biologie et dynamique des populations d'*Alestes baremoze* (Pisces,
1978 Characidae) du bassin Tchadien. Trav.Doc.ORSTOM, Paris, (98):332 p.

FAO, Report of the CECAF Working Party on regulatory measures for demersal stocks. FAO
1970 Fish.Rep., (91):24 p.

____________, Report of the second session of the FAO Fishery Committee for the Eastern
1971 Central Atlantic (CECAF) Working party on regulatory measures for demersal stocks. Rome, 22-26 March 1971. FAO Fish.Rep., (190):109 p. Issued also in French

____________, Fishery Committee for the Eastern Central Atlantic, Report of the *Ad hoc*
1978 Working Group on the assessment of cephalopod stocks. CECAF/ECAF Ser., (78/11):148 p.

____________, Fishery Committee for the Eastern Central Atlantic, Report of the Special
1980 Working Group on the cephalopod of the northern region of CECAF. CECAF/ECAF Ser., (82/24):180 pp.

____________, Yearbook of fishery statistics. Annuaire statistique des pêches. Anuario
1981 estadístico de pesca, 1980. Catches and landings. Captures et quantités débarquées. Capturas y desembarques. FAO Yearb.Fish.Stat./Annu.Stat.Pêches/Anu.Estad.Pesca, (50):385 p.

____________, Review of the state of world fishery resources. FAO Fish.Circ., (710)
1981a Rev. 2:52 p. Issued also in French, Spanish, Arabic and Chinese

____________, Fishery Committee for the Eastern Central Atlantic, Report of the Special
1982 Working Group on cephalopod stocks in the northern region of CECAF. CECAF/ECAF Ser., (82/24):178 pp. Issued also in French

Fischer, W. (ed.), 1973 FAO species identification sheets for fishery purposes. Mediterranean and Black Sea (fishing area 37). Rome, FAO, Vol. 2:pag. var.

———————, 1978 FAO species identification sheets for fishery purposes. Western Central Atlantic (fishing area 31). Rome, FAO, Vols. 1-7:pag. var.

Fischer, W. and P.J.P. Whitehead (eds), 1974 FAO species identification sheets for fishery purposes. Eastern Indian Ocean (fishing area 57) and Western Central Pacific (fishing area 71). Rome, FAO, Vol. 1:pag. var.

Fischer, W., G. Bianchi and W.B. Scott (eds), 1981 FAO species identification sheets for fishery purposes. Eastern Central Atlantic (fishing areas 34, 47 (in part)). Canada Funds-in-Trust. Ottawa, Department of Fisheries and Oceans Canada, by arrangement with the Food and Agriculture Organization of the United Nations, Vols. 1-7:pag. var.

Fiscus, C.H., 1982 Predation by marine mammals on squids on the eastern North Pacific Ocean and the Bering Sea. Mar.Fish.Rev., 44(2):1-10

Fishery Committee for the Eastern Central Atlantic (CECAF), 1976 Evaluation of the fishery resources of the Eastern Central Atlantic. Report of the third session of the Working Party on resource evaluation of the Fishery Committee for the Eastern Central Atlantic (CECAF). Rome, 9-13 February 1976. FAO Fish.Rep., (183): 135 p. Issued also in French

——————— (CECAF), 1979 Report of the *Ad hoc* Working Group on the assessment of cephalopod stocks. CECAF/ECAF Ser., (78/11):149 p. Issued also in French

——————— (CECAF/COPACE), 1981 CECAF Statistical bulletin, No. 3. Nominal catches 1969-1979. Bulletin statistique du COPACE No. 3. Captures nominales 1969-1979. CECAF Stat.Bull./Bull.Stat.COPACE, (3):211 p.

Garcia, S. and L. Le Reste, 1981 Life cycle, dynamics, exploitation and management of coastal penaeid shrimp stocks. FAO Fish.Tech.Pap., (203):215 p. Issued also in French

Garrod, D.J., 1973 Management of multiple resources. J.Fish.Res.Board Can., 30(12)Pt.2:1977-85

Grandperrin, R., 1978 Influence of currents on the production of tropical seas: consequences for fisheries. South Pac.Comm.Fish.Newsl., (17):14-20

Hatanaka, H., 1979 Studies on the fishery biology of common octopus off the northwest coast of Africa. Bull.Far Seas Fish.Res.Lab., (17):13-124

Hotta, M., 1982 The Japanese market for squid and cuttlefish. INFOFISH Market.Dig., (4):12-9

Hurley, G.V. and P. Beck, 1980 The observation of growth rings in statoliths from the Ommastrephid squid, *Illex illecebrosus*. NAFO SCR. Doc. 80/II/1, Ser. No. N027:17 p.

Hurley, G.V. and R.K. Mohn, 1979 Considerations on the management of the international squid (*Illex*) fishery in ICNAF subarea 4. Tech.Rep.Fish.Mar.Serv.Can., (833):7.1-7.14

ICNAF, 1979 International Commission for the Northwest Atlantic Fisheries. Report of Assessment subcommittee, 28 March-9 April 1979. ICNAF Sum. Doc. 79/VI/11. Ser. No. 5419

ISRA/ORSTOM, 1979 La reproduction des espèces exploitées dans le Golfe de Guinée. Rapport du Groupe de Travail ISRA-ORSTOM. Dakar 9-12 novembre 1977. Doc.Sci.Cent.Rech. Océanogr.Dakar-Thiaroye, (68):213 p.

Jones, R., 1973 Density dependent regulation of the numbers of cod and haddock. Rapp.P.-V. Réun.CIEM, 164:156-77

__________, 1976 The use of marking data in fish population analysis. FAO Fish.Tech.Pap., (153):41 p.

__________, 1981 The use of length composition data in fish stock assessment (with notes on VPA and cohort analysis). FAO Fish.Circ., (734):60 p. Issued also in Spanish

Klimaj, A., 1970 Cephalopods as by-catch in trawls from the fishing grounds extending from Rio de Oro to Cape Timiris in 1966. Rapp.P.-V.Réun.CIEM, 159:146-8

Lange, A.M. and M.P. Sissenwine, 1980 Biological considerations relevant to the management of squid (*Loligo pealei* and *Illex illecebrosus*) of the northwest Atlantic. Mar. Fish.Rev., 42(7-8):23-38

Lett, P.F., A.C. Kohler and D.N. Fitzgerald, 1975 Role of stock biomass and temperature in the recruitment of southern Gulf of St. Lawrence: Atlantic cod, *Gadus morhua*. J.Fish.Res.Board Can., 32(9):1613-28

Lipinski, M., 1978 The age of squids, *Illex illecebrosus* (Le Sueur, 1921), from their statoliths. ICNAF Res. Doc. 78/II/15, Ser. No. 5167:2 p.

MacArthur, R.H. and E.O. Wilson, 1967 The theory of island biography. Princeton, New Jersey, Princeton University Press, 203 p.

Mercer, M.C., 1974 Modified Leslie-Deluny assessments of the northern pilot whale (*Globicephalex melaena*) and annual production of the short-finned squid (*Illex illecebrosus*) based upon their interaction at Newfoundland. ICNAF Res. Doc. 74/49:14 p.

Mesnil, B., 1976 Growth and life cycle of squid, *Loligo pealei* and *Illex illecebrosus*. ICNAF Res. Doc. 76/VI/65

__________, 1977 Biological characteristics and biomass estimates of squid, *Loligo pealei* and *Illex illecebrosus*, on mid-Atlantic and southern New England shelves. ICNAF Res. Doc. 77/VI/4, Ser. No. 5012:13 p.

Mohn, R.K., 1981 Yield per recruit analysis of 4 VWX squid by simulation. NAFO SCR. Doc. 81/VI/40:16 p.

Morgan, G.R. and S. Garcia, 1981 The relationship between stock and recruitment in the shrimp stock of Kuwait and Saudi Arabia. Paper presented to the Workshop on the scientific basis for the management of penaeid shrimps, Key West, 18-24 November 1981

Navarro, F. de P., *et al.*, 1945 La pesca de arrastre en los fondos del Cabo Blanco y del banco de Argún (Africa sahariana). Trab.Inst.Esp.Oceanogr., (18):25 p.

Nigmatallin Ch. M. and A.A. Ostapenko, 1976 Feeding of *Octopus vulgaris* Lam. from the northwest African coast. ICES CM.1976/K 6:15 p.

O'Dor, R.K., *et al.*, 1979 Feeding and growth rates in captive squid (*Illex illecebrosus*) and the influence of food availability on growth. ICNAF Res. Doc. 79/II/16, Ser. No. 5342

__________, 1980 Feeding and growth in captive squid (*Illex illecebrosus*) and the influence of food availability on growth in the population. Sel.Pap.ICNAF, 6:15-21

Odum, E.P., 1965 Fundamentals of ecology. Philadelphia, W.B. Saunders Co., 546 p. 2nd ed.

Okutani, T., 1977 Stock assessment of cephalopods resources fished by Japan. FAO Fish.Tech. Pap., (173):62 p.

Pauly, D., 1979 Theory and management of tropical multispecies stocks: a review with emphasis on the Southeast Asian demersal fisheries. ICLARM Stud.Rev., (1):35 p.

Pauly, D. and N. David, 1980 A basic program for the objective extraction of growth parameters from length-frequency data. ICES, CM 1980/D:7 Statistics Comm. 14 p. (mimeo)

Pereiro, J.A. and J. Bravo de Laguna, 1979 Dinámica de la población y evaluación de los recursos del pulpo del Atlantíco centro-oriental. Bol.Inst.Esp.Oceanogr., 5(275):71-105

Pope, J., 1979 Stock assessment in multispecies fisheries, with special reference to the trawl fishery in the Gulf of Thailand. Manila, South China Sea Fisheries Development and Coordinating Programme, SCS/DEV/79/19:106 p.

Roper, C.L., M. Sweeney and C.E. Nauen, 1983 Cephalopods of the world. An illustrated and annotated species world catalogue. FAO Spec. Synopsís No. 125 (Vol.3 in Press.)

Ricker, W.E., 1975 Computation and interpretation of biological statistics of fish populations. Bull.Fish.Res.Board Can., (191):382 p.

Saila, S.B. and J.D. Parrish, 1972 Exploitation effects upon interspecific relationships in marine ecosystems. Fish.Bull.NOAA/NMFS, 70 (2):383-93

Sanders, M.J., 1979 Preliminary stock assessment for the cuttlefish *Sepia pharaonis* taken off the coast of the People's Democratic Republic of Yemen. Rome, FAO, UNDP/FAO Report, RAB/77/008, 54 p. (mimeo)

__________, 1981 Revised stock assessment for the cuttlefish *Sepia pharaonis* taken off the coast of the People's Democratic Republic of Yemen. Rome, FAO/UNDP Report, RAB/77/008:44 p. (mimeo)

Sissenwine, M.P., 1976 A review of stock size estimates of squid (*Loligo* and *Illex*) in subarea 5 and statistical area 6. ICNAF Res. Doc. 76/VI/31, Ser. No. 3811:5 p.

Smith, O.J., P.E. Roberts and R.J. Hurst, 1981 Evidence for two species of arrow squid in the New Zealand fishery. N.Z.Mar.Freshwat.Res., 15:247-53

Ssentongo, G.W. and P.A. Larkin, 1973 Some simple methods of estimating mortality rates of exploited fish population. J.Fish.Res.Board Can., 30(5):695-8

Voss, G.L., 1974 Cephalopod resources of the world. FAO Fish.Circ., (149):1-175

Vouk, A.N., 1972 The position of the long-finned squid, *Loligo pealei* Les., in the ecosystem. Tr.Vses.Nauchno-Issled.Inst.Morsk.Rybn.Khoz.Okeanogr., 58:168-76. Issued also as Transl.Ser.Fish.Mar.Serv.Can., (3977)

October 1983

SELECTED LIST OF FAO PUBLICATIONS ON FISHERY RESOURCE APPRAISAL METHODOLOGY

FAO publications on scientific aspects of fisheries are issued in the following main series of documents:

a) FAO Manuals on Fisheries Science which are priced publications.

b) FAO Fisheries Technical Papers which are normal vehicles for technical reports.

c) FAO Fisheries Circulars which are used as a repository for preliminary studies that may be reissued as Technical Papers.

Selected publications from regional projects have also been included in this list. These, however, may not be as readily available as the main series listed above.

Requests for documents should be addressed to:

Distribution and Sales Unit
Publications Division
Food and Agriculture Organization
Via delle Terme di Caracalla
00100 Rome, Italy

Requests for documents of the South China Sea Programme should be addressed to:

South China Sea Fisheries Development
and Coordinating Programme
P.O. Box 1184
MCC Makati
Metro Manila
Philippines

A list of all FAO Fisheries Department publications covering the years 1948-1978 is published as FAO Fisheries Circular (100)Rev.3. An up-dating of this is in preparation.

When documents are out of print microfiches or photocopies may be ordered from the Library and Documentation Division of FAO under the following conditions:

Photocopies can be made of items not exceeding 50 pages at US$ 2.00 for every 10 pages or less of each document.

Documents over 50 pages are only available in microfiche form of 60 pages per fiche. The cost of the first fiche is US$ 2.00 and subsequent ones US$ 1.00 each.

1. Fishery biology

Advisory Committee of Experts on Marine Resources Research (ACMRR)/Comité consultatif
1981 d'experts de la recherche sur les ressources de la mer (CCRRM)/Comité Asesor sobre Investigaciones de los Recursos Marinos (CAIRM)/, Report of the Working Party on the promotion of fishery resources research in developing countries. Fløro, Norway, 2-8 September 1979/Rome, Italy, 8-12 September 1980. Rapport du Groupe de travail sur la promotion de la recherche sur les ressources halieutiques des pays en développement. Fløro, Norvège, 2-8 septembre 1979/Rome, Italie, 8-12 septembre 1980. Informe del Grupo de Trabajo para la promocion de las investigaciones sobre recursos pesqueros en los paises en desarrollo. Fløro, Noruega, 2-8 de septiembre de 1979/Roma, Italia, 8-12 de septiembre de 1980. FAO Fish.Rep./FAO,Rapp.Pêches/FAO,Inf.Pesca, (251):235 p.

FAO, Selected references of general interest to fishery scientists (1976-77). FAO Fish.Circ.,
1977 (705):13 p.

__________, Selected references of general interest to fishery scientists: Addendum for 1977-78.
1978 FAO Fish.Circ., (705)Add.1:9 p.

Holden, M.J. and D.F.S. Raitt (eds), Manual of fishery science. Part 2. Methods of resource
1974 investigations and their application. FAO Fish.Tech.Pap., (115)Rev.1:214 p. Issued also in French and Spanish

Kesteven, G.L., Manual of fishery science. Part 1. An introduction to fisheries science. FAO
1973 Fish.Tech.Pap., (118):43 p. Issued also in French and Spanish

Laevastu, T., Manual of methods in fisheries biology. FAO Man.Fish.Sci., (1):10 fasc. Issued also in
1965 French. Spanish version published for FAO by Editorial Acribia, Zaragoza, Spain

Simpson, A.C., The role of research in fisheries development. FAO Fish.Circ., (720):17 p.
1977

Tomczak, G.H., Environmental analyses in marine fisheries research. FAO Fish.Tech.Pap., (170):
1977 141 p.

2. Stock assessment and fishery management

ACMRR Working Party on the Scientific Basis of Determining Management Measures, Report of the
1980 ACMRR Working Party on the scientific basis of determining management measures. Hong Kong, 10-15 December, 1979. FAO Fish.Rep., (236):149 p.

Beddington, J.R. and J.G. Cooke, The potential yield of fish stocks. FAO Fish.Tech.Pap.,
1983 (242):47 p.

Beverton, R.J.H. and S.J. Holt, Manual of methods of fish stock assessment. Part 2. Tables of yield
1966 functions. Manuel sur les méthodes d'évaluation des stocks ichthyologiques. Partie 2. Tables de fonctions de rendement. Manual de métodos para la evaluacion de los stocks de peces. Parte 2. Tablas de functiones de rendimiento. FAO Fish.Tech.Pap./FAO, Doc.Tech.Pêches/FAO,Doc.Téc.Pesca, (38)Rev.1:67 p.

Burke, W.T., Fisheries regulations under extended jurisdiction and international law. FAO Fish.
1982 Tech.Pap., (223):23 p.

Caddy, J.F. (ed.), Provisional world list of computer programmes for fish stock assessment and their
1982 availability by country and fisheries institute. FAO Fish.Circ., (746):51 p.

__________, Some considerations relevant to the definition of shared stocks and their allocation
1982a between adjacent economic zones. FAO Fish.Circ., (749):44 p. Issued also in Spanish

__________ (ed.), Advances in assessment of world cephalopod resources. Progrès réalisés dans
1983 l'évaluation des ressources mondiales de céphalopodes. Progresos realizados en la evaluacion mundial de cefalopodos. FAO Fish.Tech.Pap./FAO,Doc.Tech.Pêches/FAO, Doc.Téc.Pesca, (231):452 p.

* CIDA/FAO/CECAF, Selected lectures from the CIDA/FAO/CECAF seminar on fishery resource
1980 evaluation. Casablanca, Morocco, 6-24 March 1978. Rome, FAO, Canada Funds-in-Trust, FAO/TF/INT/180(c) (CAN)Suppl.:166 p. French version in preparation

Csirke, J., Introduccion a la dinamica de poblaciones de peces. FAO,Doc.Téc.Pesca, (192):82 p.
1980

FAO, Monitoring of fish stock abundance: the use of catch and effort data. A report of the ACMRR
1976 Working Party on fishing effort and monitoring of fish stock abundance. Rome, Italy, 16-20 December, 1975. FAO Fish.Tech.Pap., (155):101 p.

* ___________, Models for fish stock assessment. FAO Fish.Circ., (701):122 p. Issued also in French
1978

___________, Some scientific problems of multispecies fisheries. Report of the expert consultation
1978a on management of multispecies fisheries, Rome, Italy, 20-23 September 1977. FAO Fish.Tech.Pap., (181):42 p. Issued also in French

___________, Methods of collecting and analysing size and age data for fish stock assessment. FAO
1981 Fish.Circ., (736):100 p. Issued also in French and Spanish

Garcia, S. and L. Le Reste, Life cycles, dynamics, exploitation and management of coastal penaeid
1981 shrimp stocks. FAO Fish.Tech.Pap., (203):215 p. Issued also in French

* Gulland, J.A., Manual of methods for fish stock assessment. Part 1. Fish population analysis. FAO
1969 Man.Fish.Sci., (4):154 p. Issued also in French. Spanish version published for FAO by Editorial Acribia, Zaragoza, Spain

___________, Guidelines for fishery management. Rome, FAO, Indian Ocean Programme, IOFC/
1972 DEV/74/36:84 p.

___________, Some introductory guidelines to management of shrimp fisheries. Rome, FAO, Indian
1972a Ocean Programme, IOFC/DEV/72/24:12 p.

* ___________, Goals and objectives of fishery management. FAO Fish.Tech.Pap., (166):14 p. Issued
1977 also in French and Spanish

___________, Some problems of the management of shared stocks. FAO Fish.Tech.Pap., (206):22 p.
1980 Issued also in French

___________, Stock assessment: why? FAO Fish.Circ., (759):18 p. Issued also in French
1983

Hoenig, J.M. and S.B. Saila, A programmed learning guide for fishery managers in the fundamentals
1983 of stock assessment. FAO Fish.Circ., (762):49 p.

Jones, R., Mesh regulation in the demersal fisheries of the South China Sea area. Manila, South
1976 China Sea Fisheries Development and Coordinating Programme, SCS/76/WP/34:79 p.

___________, The use of marking data in fish population analysis. FAO Fish.Tech.Pap., (153):42 p.
1976a

___________, Materials and methods used in marking experiments in fishery research. FAO
1979 Fish.Tech.Pap., (190):133 p.

___________, The use of length composition data in fish stock assessments (with notes on VPA and
1981 cohort analysis). FAO Fish.Circ., (734):55 p. Issued also in French and Spanish

Pauly, D., Some simple methods for the assessment of tropical fish stocks. FAO Fish.Tech.Pap.,
1980 (234):52 p. Issued also in Spanish. French version in preparation

Pearse, P.H., Regulation of fishing effort: with special reference to Mediterranean trawl fisheries.
1980 FAO Fish.Tech.Pap., (197):82 p. Issued also in French

Pope, J.A. et al., Manual of methods for fish stock assessment. Part 3. Selectivity of fishing gear.
1975 FAO Fish.Tech.Pap., (41)Rev.1:46 p.

Pope, J.G., Stock assessment in multispecies fisheries with special reference to the trawl fishery in
1979 the Gulf of Thailand. Manila, South China Sea Fisheries Development and Coordinating Programme, SCS/DEV/79/19:106 p.

Saila, S.B., Importance and assessment of discards in commercial fisheries. FAO Fish.Circ.,
1983 (765):62 p.

Troadec, J.-P., Introduction à l'aménagement des pêcheries: Intérêt, difficultés, et principales
1982 méthodes. FAO,Doc.Tech.Pêches, (224):64 p.

3. Resources surveys

Alverson, D.L., Field surveys and the survey and charting of resources. Rome, FAO, Indian Ocean
1971 Programme, IOFC/DEV/71/6:22 p.

Bazigos, G.P. (ed.), A manual on acoustic surveys. Sampling methods for acoustic surveys.
1981 CECAF/ECAF Ser., (80/17):137 p.

Burczynski, J., Introduction to the use of sonar systems for estimating fish biomass. FAO
1982 Fish.Tech.Pap., (191)Rev.1:89 p. Issued also in French and Spanish. Also to be published in Japanese under an agreement between FAO and the Japan Fisheries Resource Conservation Association

Forbes, S.T. and O. Nakken (eds), Manual of methods for fisheries resource survey and appraisal. Part
1972 2. The use of acoustic instruments for fish detection and abundance estimation. FAO Man.Fish.Sci., (5):138 p. Issued also in French and Spanish

Grosslein, M.D. and A. Laurec, Bottom trawl surveys design, operation and analysis. CECAF/ECAF
1982 Ser., (81/22):25 p. Issued also in French

* Gulland, J.A., Manual of methods for fisheries resource survey and appraisal. Part 5. Objectives and
1975 basic methods. FAO Fish.Tech.Pap., (145):29 p.

Mackett, D.J., Manual of methods for fisheries resource survey and appraisal. Part 3. Standard
1973 methods and techniques for demersal fisheries resource surveys. FAO Fish.Tech.Pap., (124):39 p.

* Saville, A. (ed.), Survey methods of appraising fishery resources. FAO Fish.Tech.Pap., (171):76 p.
1977 Issued also in French and Spanish

Smith, P.E. and S.L. Richardson, Standard techniques for pelagic fish egg and larva surveys. FAO
1977 Fish.Tech.Pap., (175):100 p. Issued also in Spanish

__________, Selected bibliography on pelagic fish egg and larva surveys. Bibliographie selectionée
1979 sur les prospections d'oeufs et de larves de poisson pélagiques. Bibliografia seleccionada sobre riconocimientos de huevos y larvas de peces pelagicos. FAO Fish.Circ./FAO, Circ.Pêches/FAO, Circ.Pesca, (706):97 p. (Trilingual)

Ulltang, O., Methods of measuring stock abundance other than by the use of commercial catch and
1977 effort data. FAO Fish.Tech.Pap., (176):23 p. Issued also in French and Spanish

Venema, S.C. (comp.), A selected bibliography of acoustics in fisheries research and related fields.
1982 FAO Fish.Circ., (748):154 p.

4. Fishery statistics

Banerji, S.K., Frame surveys and associated sample survey designs for the assessment of marine fish
1974 landings. Rome, FAO, Indian Ocean Programme, IOFC/DEV/74/39:15 p.

__________, Improvement of national fishery statistics. Rome, FAO, Indian Ocean Programme,
1975 IOFC/DEV/75/41:15 p.

Bazigos, G.P., The design of fisheries statistical surveys - inland waters. FAO Fish.Tech.Pap.,
1974 (133):122 p. Issued also in French and Spanish

__________, Applied fishery statistics. FAO Fish.Tech.Pap., (135):164 p. Issued also in French and
1974a Spanish

__________, Applied fishery statistics: vectors and matrices. FAO Fish.Tech.Pap., (135)Suppl.1:
1975 34 p.

__________, The design of fisheries statistical surveys - inland waters. FAO Fish.Tech.Pap.,
1976 (133)Suppl.1:46 p.

* __________, Mathematics for fishery statisticians. FAO Fish.Tech.Pap., (169):183 p.
1977

* Brander, K., Guidelines for collection and compilation of fishery statistics. FAO Fish.Tech.Pap.,
1975 (148):46 p.

FAO, The collection of catch and effort statistics. FAO Fish.Circ., (730):63 p. Issued also in
1980 Spanish. French version in preparation

* Gulland, J.A., Manual of sampling and statistical methods for fisheries biology. Part 1. Sampling
1966 methods. FAO Man.Fish.Sci., (3):87 p. Issued also in French and Spanish. Published in Portuguese by the Superintendéncia do Desenvolvimento do Nordeste (SUDENE), Recife, Brasil, in 1966

Moller, F., Manual of methods in aquatic environmental research. Part 5. Statistical tests. FAO
1979 Fish.Tech.Pap., (182):131 p.

5. Inland fisheries

Backiel, T. and R.L. Welcomme (eds), Guidelines for sampling fish in inland waters. EIFAC
1980 Tech.Pap., (33):176 p.

Bhukaswan, T., Management of Asian reservoir fisheries. FAO Fish.Tech.Pap., (207):69 p.
1980

FAO, Comparative studies on freshwater fisheries. Report of a Workshop held at the Istituto
1980 Italiano di Idrobiologia. Pallanza, Italy, 4-8 September 1978. FAO Fish.Tech.Pap., (198):46 p.

Kapetsky, J.M., Some considerations for the management of coastal lagoon and estuarine fisheries.
1981 FAO Fish.Tech.Pap., (218):47 p. Issued also in Spanish and French. Arabic version in preparation

Welcomme, R.L. (comp.), Fishery management in large rivers. FAO Fish.Tech.Pap., (194):60 p.
1979 Issued also in Spanish

__________, Cuencas fluviales. FAO,Doc.Téc.Pesca, (202):62 p.
1980

Welcomme, R.L. and H.F. Henderson, Aspects of the management of inland waters for fisheries.
1976 FAO Fish.Tech. Pap., (161):40 p. Issued also in French and Spanish

Note:

The documents marked with an asterisk were translated into Chinese for use at a UNDP/FAO training course in fish stock assessment held in Shanghai in 1980.

Tipo-lito SAGRAF - Napoli

M-43
ISBN 92-5-001431-7